The Prudent Parent

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Phenotypic Flexibility in Reproductive Effort Across Breeding Stages in Birds

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Prof. Dr. Carolus P. van Schaik (Vorsitz)

Dr. Michael Griesser (Leitung der Dissertation)

Dr. Arpat Ozgul

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Summary

Life history theory provides a framework to understand how organisms allocate their limited resources into growth, survival and reproduction to maximize fitness. Life history traits are predicted to covary across a fast-slow pace of life spectrum; a fast pace of life is usually observed in small species with low survival rates and high fecundity, and a slow pace of life tends to be observed in large species with high survival and low fecundity. However, species that are similar among these traits can show differences in other aspects of their life history, and the study of how traits vary in relation to each other and to the environment is essential for understanding evolution in general.

The aim of this dissertation is to elucidate interspecific variation in reproductive performance across nest stages in birds, and to identify sources of variation in reproductive flexibility. Reproductive effort in birds has played a prominent role in the development of life history theory, with a focus on the evolution of clutch size. Yet, it is variation in reproductive success that drives natural selection, which in turn shapes reproductive investment as a whole, with fecundity (i.e., the number of eggs laid) functioning as only one of the means of optimizing that investment. Costs of reproduction accumulate over the nesting cycle, and reproductive demands at later stages of nesting may feed-back to affect the evolution of fecundity, illuminating the need for comparative studies that explore reproductive effort beyond egg-laying. Furthermore, empirical studies of additional components of reproductive effort, such as egg or offspring size, developmental rates, and parental care behavior remain rare.

In Chapter 2, I examine interspecific variation in reproductive performance across breeding stages in birds. My findings indicate that annual fecundity (i.e., number of eggs) and survival of dependent offspring have different constraints. Interspecific variation in annual fecundity correlates with key intrinsic species traits (life-history pace, developmental mode, and migratory habits), while the relative success at each stage of nesting depends on the breeding ecology of a species (i.e., latitude, nest predation and habitat specialization). Importantly, the proportion of offspring that survive is unrelated to annual fecundity, suggesting that females may not be able to regulate clutch

size according to the current conditions. These results emphasize that the number of eggs an individual lays may be a poor proxy for fitness.

Life history traits do not only vary between species; they are also subject to variation within individuals and populations. Breeding conditions can be highly dynamic, resulting in no single phenotype being consistently optimal. Phenotypic flexibility is a means of responding to changes in current conditions and is an integral facet of life history, which should be considered alongside mean trait values. Yet, relatively little is known about the extent to which phenotypic flexibility varies, and even less about the causes of variation in phenotypic flexibility, across individuals or species. In the subsequent chapters of this thesis, I explore how reaction norms to variable breeding conditions differ among and within species, and examine potential causes and consequences of flexibility in reproductive decisions, through a series of experiments in wild bird populations.

In Chapter 3, I examine how changes in the perceived risk of nest predation prior to egg-laying affect parental investment decisions and downstream nesting success. In Chapter 4, I use a long-term dataset to examine reproductive effort in good and bad years. I then discuss the results of a field study in which we experimentally reduced the condition of females before egg laying and examined its effect on the survival of adult birds and offspring. Finally, in Chapter 5, I assess sources of interspecific variation in responses to an experimentally increased cost of parental care by handicapping one parent of biparental pairs in five bird species. The findings of these studies highlight that the degree to which avian parents can, or will, adjust their reproductive allocation differs greatly among species. In particular, species with long parental care periods emerged as the most sensitive to adverse conditions during the breeding season.

The results presented in this dissertation shed new light on life history trade-offs and how they interact with environmental factors to influence reproductive decisions and productivity in birds. The findings demonstrate that costs of reproduction can be mitigated through condition-dependent reproductive allocation. While typical proxies for life history pace (e.g., adult survival) primarily set the upper limit for the number of offspring a given species can reasonably care for in a reproductive event, flexibility of reproductive allocation under adverse breeding conditions

primarily depended on the duration of parental care (e.g., offspring developmental time, duration of parent-offspring association). Finally, these findings highlight the need to assess productivity independently at each reproductive stage, with more attention to reproductive output than initial allocation, and that greater attention should be paid to the variance of reproductive traits.

The modern world is changing at an unprecedented pace and scale, and human activities have a profound impact on ecosystems worldwide. Behavioral flexibility may provide a mechanism for dealing with highly variable conditions for many animals, as opportunities for dispersal may be limited and evolutionary processes may not be able to keep up with the current rates of environmental change. As the world becomes increasingly dominated by humans, it will be crucial to understand whether and how organisms can cope with these changes. The results presented here demonstrate that species vary in the strength of their responses to heterogeneity in breeding conditions and reveal some potential causes of that variation. Improved knowledge of these processes will be crucial to projecting the prospects for species in the long term and, where possible, to counteract the loss of biodiversity.

Zusammenfassung

Die *Life-history Theorie* erklärt, wie Organismen begrenzte Ressourcen in Wachstum, Überleben und Fortpflanzung investieren und verteilen um maximale Fitness zu erzielen. Je nachdem wie Organismen diesen *Trade-off* lösen, investieren sie ihre Energie mehr in jetzige oder zukünftige Fortpflanzung. Kleine Arten haben meistens eine höher Fortpflanzungsrate aber dafür eine kürzere Lebensspanne; größere Arten haben meistens eine niedrige Fortpflanzungsrate aber eine längere Lebensspanne. Es gibt jedoch Arten, welche ähnliche Größen, Überlebenschancen oder Fortpflanzungsraten haben und sich dafür in anderen Merkmalen unterscheiden. Entsprechend ist es wichtig herauszufinden, wie die unterschiedlichen Merkmale in Relation zueinander und zur Umwelt variieren, um evolutive Vorgänge zu verstehen.

Das Ziel dieser Dissertation ist es zwischenartliche Variation in reproduktive Investitionen während den verschiedenen Neststadien von Vögel zu erläutern und Quellen, die zur Variation reproduktiver Flexibilität führen, zu identifizieren. Reproduktive Investitionen bei Vögeln, insbesondere Variation in der Gelegegröße, spielte historisch eine wichtige Rolle bei der Entwicklung der *Life-history Theorie*. Für die Fitness eines Individuums ist jedoch nicht die Gelegegröße, sondern die Anzahl der Nachkommen entscheidend. Aus diesem Grund sind vergleichenden Studien, die beides die Gelegegröße und die Anzahl der Nestlinge in Betracht ziehen wichtig.

In Kapitel 2 untersuche ich zwischenartliche Variation im Fortpflanzungsverhalten in verschiedenen Brutstadien von Vögeln. Meine Resultate zeigen, dass die Anzahl gelegter Eier und das Überleben des Nachwuchses unterschiedlichem Selektionsdruck ausgesetzt ist. Die zwischenartliche Variation der jährlichen Fruchtbarkeit korreliert mit intrinsischen Artenmerkmalen (Lebensrhythmus, Entwicklungsstadium und Zugverhalten), während der relative Erfolg jedes Brutstadiums von der Brutökologie einer Art abhängt (z.B. Breitengrad, Nestprädation und Lebensraumspezialisierung). Die Proportion der überlebenden Nachkommen ist jedoch unabhängig von der jährlichen Fruchtbarkeit, was darauf schliessen lässt, dass die

Weibchen keinen Einfluss darauf haben die Gelegegröße den momentanen Umständen anzupassen.

Life-history Merkmale können innerhalb von Individuen und Populationen variieren. Brutbedingungen können sich schnell verändern und es gibt keinen Phänotyp der sich immer optimal verhält. Phänotypische Flexibilität ist eine Anpassung um auf verändernde Bedingungen zu reagieren und ist ein integraler Aspekt der *Life-history*. Es ist jedoch relativ wenig bekannt wie sich phänotypische Flexibilität verändert und noch weniger, was die Gründe für die phänotypische Variation über Individuen oder Arten hinweg sind. In den folgenden Kapiteln meiner Dissertation versuche ich herauszufinden, wie sich die Reaktionsnorm im Bezug auf unterschiedliche Brutbedingungen zwischen und innerhalb von Arten unterscheiden und untersuche potentielle Ursachen und Konsequenzen flexibler Reproduktionsentscheide anhand einer Reihe von Experimenten wild lebender Vogelpopulationen.

In Kapitel 3 untersuche ich, wie sich die elterliche Fürsorge aufgrund des wahrgenommenen Prädationsrisiko bevor dem Eierlegens auswirkt. In Kapitel 4 analysiere ich anhand eines Langzeitdatensatzes einer langlebigen Vogelart reproduktive Investitionen in guten und schlechten Jahren. Dann diskutiere ich die Ergebnisse einer Feldstudie, in welcher wir die Kondition von Weibchen vor dem Eierlegen experimentell reduzierten und dessen Effekt auf das Überleben der erwachsenen Vögel und der Nachkommen. In Kapitel 5 untersuche ich die Ursache zwischenartlicher Variation als Antwort auf experimentell erhöhter Kosten elterlicher Fürsorge, indem wir jeweils von fünf verschiedenen Vogelarten einen Elternteil eines Paares manipuliert haben. Die Resultate dieser Studie zeigen inwieweit Vogeleltern die Reproduktionskosten anpassen können und wollen und wie stark dies von der Vogelart abhängt. Insbesondere zeigt es, dass Vogelarten mit einer langen Fürsorgeperiode viel sensibler auf ungünstige Bedingungen während der Brutsaison reagieren.

Die Resultate dieser Dissertation werfen neues Licht auf *Life-history trade-offs* und wie diese mit Umweltfaktoren interagieren und Fortpflanzungsentscheide und -produktivität beeinflussen. Die Ergebnisse zeigen, dass die Reproduktionskosten durch zustandsbedingte Reproduktionsverteilung abgeschwächt werden können. Während typische Anhaltspunkte des

Lebensrhythmus (z.B. das Überleben der Eltern) die obere Grenze für die Anzahl der Nachkommen einer bestimmten Art festlegen, ist die flexible Reproduktionsverteilung unter unbeständigen Brutbedingungen vor allem durch die Voraussetzungen elterlicher Sorge bestimmt (z.B. Entwicklungszeit des Nachwuchses, Dauer der Brutpflege). Diese Ergebnisse heben hervor, dass man dem Bruterfolg mehr Bedeutung beimessen soll als der Gelegegröße und dass diese Bedeutung auch in die Varianz der Fortpflanzungsmerkmale einfliessen soll.

Die Ergebnisse dieser Dissertation können wichtige Auswirkungen für den Naturschutz haben. Die moderne Welt verändert sich in unvorhersehbarer Geschwindigkeit und Maß, und menschliche Aktivitäten können erheblichen Einfluss haben auf das weltweite Ökosystem. Flexibilität im Verhalten können eine wichtige Rolle spielen, um mit höchst variablen Bedingungen umzugehen, gerade wenn die Möglichkeiten zur Ausbreitung limitiert sind und evolutive Prozesse nicht hinreichend sind, um mit der schnellen Umweltveränderung Schritt zu halten. Da die Welt vermehrt vom Menschen dominiert wird, ist es wichtig zu verstehen, ob und wie Organismen mit diesen Veränderungen umgehen. Meine Resultate zeigen, dass Arten sich in der Stärke der Antwort auf Heterogenität in den Brutbedingungen unterscheiden und potentielle Gründe für diese Variation aufzeigen. Verbessertes Wissen dieser Prozesse ist wichtig in Hinsicht auf die Zukunftsaussichten der Arten und lassen uns im besten Falle den Verlust der Biodiversität verhindern.

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Chapter 1

Thesis Overview

Chapter 1

1.1 General Introduction

The evolution of life histories

A central goal of evolutionary biology is to elucidate why life histories vary so immensely among organisms. An evolutionarily ideal organism, known as a "Darwinian demon", would simultaneously maximize all aspects of its reproductive performance and could hypothetically exist if evolutionary processes were entirely unconstrained (Law 1979). This "demon" would reproduce immediately upon birth, produce an infinite number of offspring, and live indefinitely. Such an organism is, of course, nonexistent. There are physiological and ecological constraints on reproductive and survival schedules that result in a broad range of strategies organisms employ to optimize fitness under the circumstances in which they have evolved. The problem that organisms face is to optimize combinations of traits; solutions arise in the form of tradeoffs which differ between populations and environments.

Life history theory provides a framework to understand how organisms allocate limited resources into growth, survival and reproduction to maximize fitness (Williams 1966, Stearns 1992, Roff 1993). A main tenet of life history theory is that a given level of reproductive effort affects future reproduction more greatly in long-lived than in short-lived species. Thus, long-lived species are expected to minimize costs of reproduction in a current reproductive event in favor of their survival, while short-lived species are expected to favor current reproduction, even at the expense of their own survival.

Life history traits generally covary across a fast-slow pace of life spectrum and are composed of a broader suite of traits than fecundity and adult survival (Roff 1993). A fast pace of life is usually observed in small species with low survival rates and high fecundity, and species with a slow pace of life tend to be large and have high survival paired with low fecundity. However, species that are similar in size, survival prospect, or fecundity can still show major differences in other life history traits (e.g., Martin 2004). Additional components of reproductive effort such as egg/offspring size, developmental rates, and parental care behavior may play important roles in the evolution of life

histories. Yet comparative studies of these traits, and how they interact with each other, are relatively rare.

Theoretical work has made great strides in predicting optimal reproductive allocation under diverse conditions and life-history trajectories across organisms and lineages (e.g., Schaffer 1974, Kozłowski 1992, Brommer 2000). Broad empirical comparisons rely on analogous traits in different taxa, yet measures of traits are often incompatible between taxa. For example, in many organisms, reproductive productivity is measured at the end of parental investment, e.g., the yield of seeds in plants (Shaanker et al. 1988) or the number of weaned offspring in mammals (Hamel et al. 2010). Egg-laying organisms that lack parental care, such as many reptiles, amphibians, fish and insects, are most analogous to plants in their breeding cycle, as their reproductive effort is complete after oviposition (Wiens 1984). However, nearly all birds, as well as numerous other egg-laying organisms, require continued parental effort after egg-laying. Yet, it is common to measure reproductive productivity in these animals as the number of eggs (e.g., Elgar 1990, Jetz et al. 2008, Gilbert and Manica 2010), which ignores the parental effort dedicated to raising offspring, as well as ecological factors that can strongly influence reproductive success. In some organisms (particularly long-lived birds and mammals), parental investment can even persist after the nutritional independence of offspring (Clutton-Brock 1991), which is likely to influence the optimal allocation of energy to various reproductive functions (Drobniak et al. 2015).

Variation in reproductive success drives natural selection, which in turn shapes reproductive investment as a whole, with fecundity functioning as only one means of optimizing that investment (Morris 1987). If constraints to success after oviposition or birth differ from those that affect fecundity, erroneous conclusions may be drawn for explanations of general patterns of life-history evolution.

Phenotypic flexibility in reproductive traits

A number of studies have demonstrated that life history traits are subject to variation within and between individuals of the same species, contingent upon proximate factors. Breeding conditions can be highly dynamic, resulting in no single phenotype being consistently optimal, and phenotypic

plasticity is a means of tracking, and responding to, changes in conditions (West-Eberhard 1989). Phenotypic flexibility (i.e., continuous, reversible within-individual variation, Piersma and Drent 2003) is a form of plasticity that can be particularly advantageous under rapidly and unpredictably varying conditions. Indeed, models predict that the reproductive decisions of an individual should be adjusted to external conditions (e.g., food availability, predation risk, weather conditions), and intrinsic properties (e.g., individual body condition) (e.g., Schaffer 1974, McNamara and Houston 1996, Berrigan and Scheiner 2004). In general, research suggests that a propensity for flexibility differs both among individuals within a species (Clutton-Brock 1988) and within life history traits among species (Pigliucci 2005). Thus, the same life history trait may be canalized in one species but relatively plastic in another. Although phenotypic flexibility can be essential to dealing with environmental changes, relatively little is known about the extent to which phenotypic flexibility varies, and even less about the causes of variation in phenotypic flexibility, at the individual or species level.

Phenotypic plasticity may be adaptive, maladaptive or neutral with regard to an individual's fitness. Plasticity is considered adaptive if it allows individuals to achieve higher fitness by tolerating a broader range of environmental conditions (Ghalambor et al. 2007). Although poor breeding conditions have negative fitness consequences in many species (Metcalfe and Monaghan 2001, Cam and Aubry 2011, but see Drummond et al. 2011), flexibility of reproductive allocation, through condition-dependent decision making, may offset reproductive costs to the survival and lifetime fitness of breeders (Descamps et al. 2011). Theory predicts that short-lived species, who prioritize current reproduction, exhibit low variance of reproductive allocation but high variance of adult survival, while the reverse is expected for long-lived species. Consequently, the detection of costs associated with reproduction, and the observed relationships between life history traits, will depend on both the variance of breeding conditions (van Noordwijk and de Jong 1986) and the variance of the trait observed (Hamel et al. 2010) and is accordingly predicted to be strongly tied to the pace of life (Fig. 1).

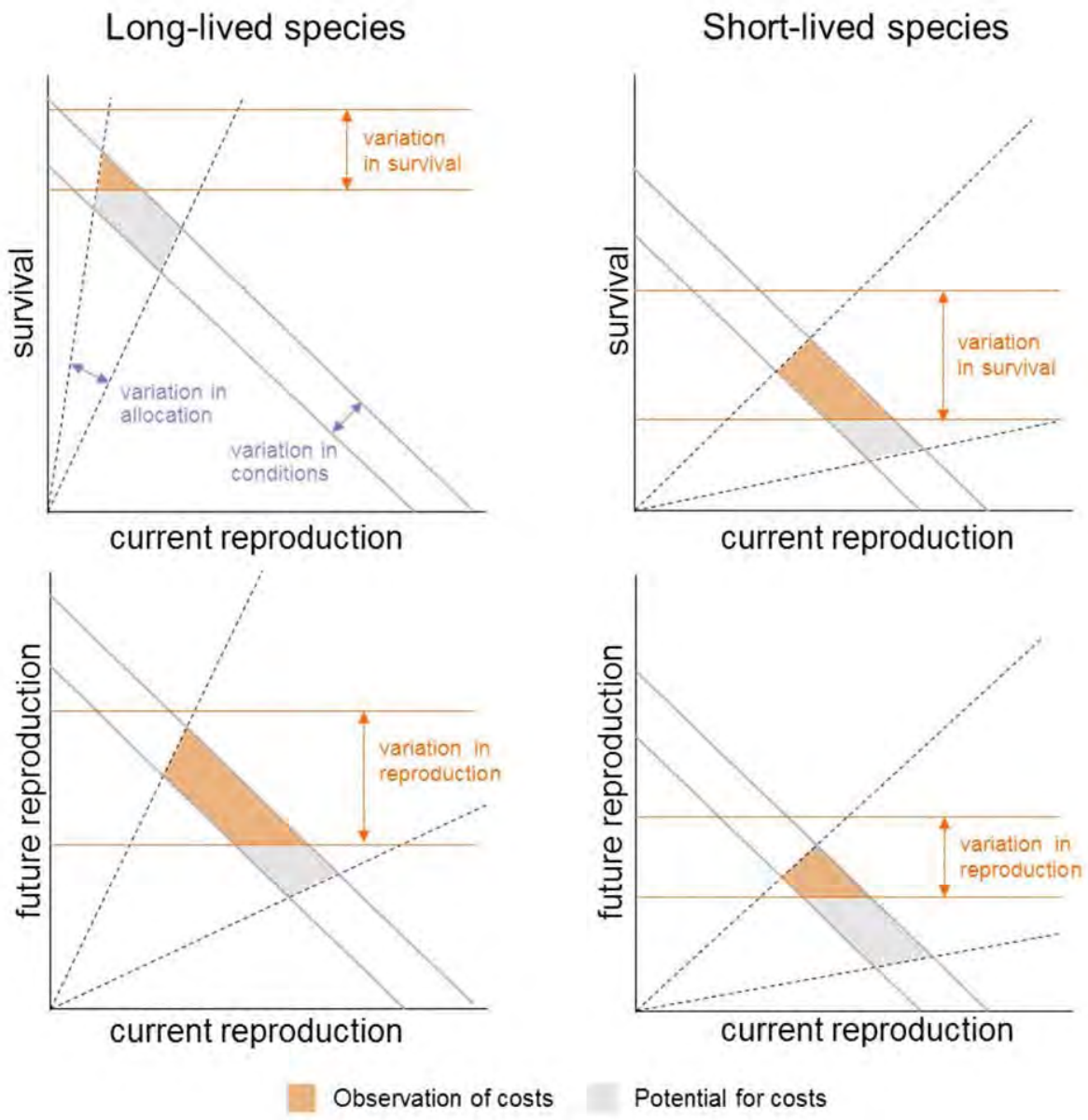

Figure 1: Variation in life history traits. Relationships between life history traits are more likely to be observed if there is a high variance of the trait in the population. Adapted from Hamel et. al 2010.

Chapter 1

Variation in flexibility is often studied using a "reaction norm" approach, which generates empirical functions of responses across environmental gradients (de Jong 1990, West-Eberhard 2003, Pigliucci 2005). Reaction norms can be measured at the individual level or be averaged across populations to investigate how individuals and species vary in their plastic responses to environmental variation. Investigations of flexible reproductive effort rely on a few key experimental paradigms. At the individual level, longitudinal studies of individuals provide repeated measures of reproductive effort by the same individual under varying conditions. At the species level, comparative studies examine evolutionary sources of interspecific differences in flexibility by testing the roles of species-specific traits on species-level variance in reproductive effort or performance. At either level, experimental tests which alter breeding conditions are valuable for examining the flexibility of responses (reaction norms) to variable demands of reproduction.

Lessons from avian life history research: don't count your chicks before they hatch

Life history traits are critical components of fitness, thus the study of how different traits vary in relation to each other and to the environment is essential for understanding evolution in general. Reproductive effort in birds has played a particularly prominent role in the early development of life history theory (Partridge and Harvey 1988, Martin 2004). Much of the pioneering work on variation in life history traits (Moreau 1944, Lack 1947, Skutch 1949) focused on the diversity of clutch sizes of birds, describing the broad patterns of variation and providing hypotheses to explain the variation, such as food limitation (Lack 1954, Cody 1966) and nest predation (Perrins 1977, Slagsvold 1982). These early studies laid the foundation for decades of theoretical and empirical investigations of life history variation across many taxa, and life history evolution remains an active avenue of investigation in avian studies. However, progress from the early days of examining reproductive effort in terms of clutch size variation in birds has been relatively slow, hindered by a lingering attention to mean values of fecundity and a small set of potential selection pressures (Martin 2004). Examination of alternative sets of traits and their associations, and additional selection pressures, holds the potential for avian studies to play a key role in further advancing evolutionary theory and understanding.

Thesis Overview

Individuals must decide how much energy to allocate to reproduction on a whole, and also must choose how to distribute that energy among the different components of reproduction (i.e., egg production, incubation, post-hatching parental care). Each stage of reproduction comes with costs, which accumulate over a breeding cycle, and theories of reproductive allocation in birds predict that clutch size trades off with the probability of juvenile survival to independence (Lack 1947, Morris 1987, Mangel et al. 1994). Field studies of individual species have demonstrated that individuals can trade-off their allocation to reproductive effort between stages (Heaney and Monaghan 1996, Russell et al. 2007), confirming that the level of investment at one reproductive stage does not necessarily translate into reproductive success (Murray Jr 2000). Environmental conditions and reproductive demands at later stages of nesting may feed-back to affect the evolution of clutch sizes (Morris 1987), further illuminating the need for comparative studies that explore reproductive effort and performance across breeding stages.

Reproductive flexibility is an integral facet of life history, and should be considered alongside mean trait values. The evolution of plasticity may occur independently of, or jointly with, changes in the mean trait value, and it is often argued that the mean trait value and its reaction norm should be considered as separate traits (De Jong 2005, Ghalambor et al. 2007). In birds, the majority of studies have focused on interspecific differences in average values of reproductive performance, but in recent years there has been a growing interest in interspecific variation in reproductive flexibility (Vézina and Salvante 2010). Several single species studies demonstrated that birds are capable of assessing their breeding condition and adjusting their reproductive investment accordingly. For example, changes in nest predation risk have resulted in parents altering their clutch size, egg size, incubation behavior, and provisioning behavior in ecological time (Lima 2009). Similarly, changes in temperature (Salvante et al. 2007), food availability (Clifford and Anderson 2001) and parental body condition (Chastel et al. 1995) have also been shown to affect reproductive decisions in birds. Few comparative studies have attempted to answer how, and why, species differ in the flexibility of their responses to adverse conditions (e.g., Ghalambor et al. 2013, Royle et al. 2014, LaManna and Martin 2016). A greater recognition of the flexibility expressed in

reproduction across species can help us to understand how species cope with rapidly changing environments and what they require to maintain healthy populations.

1.2 Aims and Outline of Thesis

The aim of this dissertation is to disentangle the sources of variation in reproductive flexibility and performance in birds among nest stages. There are three fundamental components to life-histories: the environment, the intrinsic (life-history) traits of the species, and variation in reproductive performance (Ricklefs 2000). These components form an intertwined network of selection pressures (Figure 2): the environment and species traits affect individual performance, which in turn feeds-back to influence species traits (through genetic variation in fitness and consequent evolutionary processes) and the environment (through population dynamics). In addition, the environment can influence life history traits through phenotypic plasticity.

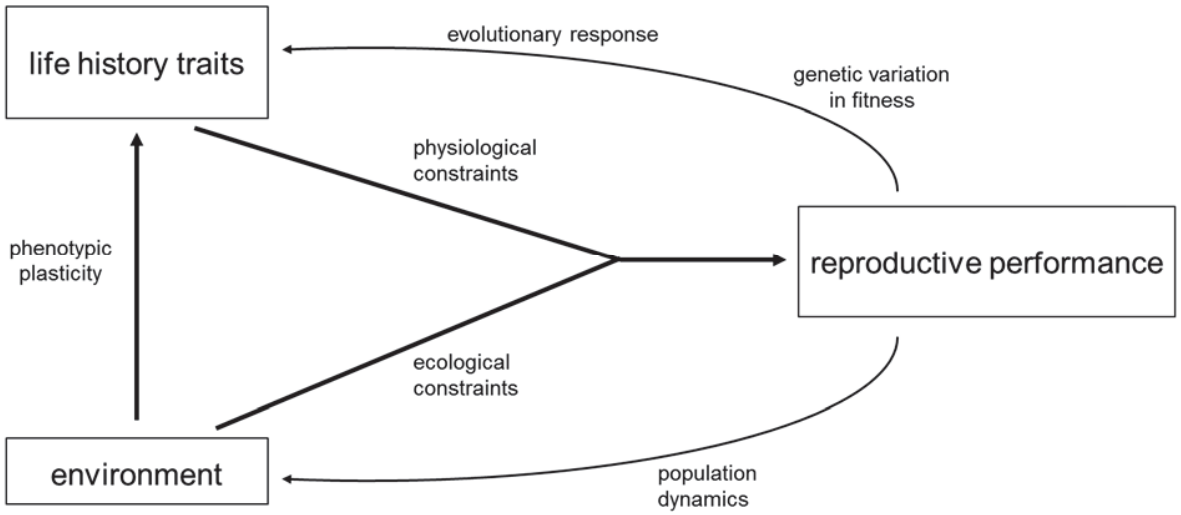

Figure 2: Life histories rely on three linked components. Variation in individual reproductive performance leads to genetic variation in fitness, which sets the stage for evolutionary responses of the population to variation in the environment. Environmental variation feeds-back to modify reproductive performance (through ecological constraints such as resource availability, predation pressure, population density or weather) and life-history traits (through phenotypic plasticity). Bold arrows indicate the focus of this thesis. Adapted from Ricklefs 2000.

Thesis Overview

In this thesis, I principally test how species traits and the environment interact to influence reproductive performance in ecological time, with implications for the feedback of reproductive performance on species traits and the environment. To explore how parents differentially adjust to unfavorable breeding conditions, I conducted a series of comparative studies and experiments which focused on various adversities along the breeding cycle of birds.

In Chapter 2, I investigate the general patterns of variation in reproductive allocation and performance among bird species. While most previous studies have assessed variation in allocation at a single reproductive stage, often early in a reproductive cycle, annual reproductive success is a better fitness proxy than fecundity (i.e., the number of eggs or propagules). Thus, it can be critical to look beyond fecundity to understand the evolution of life-histories and how life history components interact with each other. Furthermore, considering that selection acts on individual breeders, not nests or eggs, measures of annual productivity are more pertinent to demographic and evolutionary studies than the more common study of single reproductive events, yet they are relatively rare in the avian literature. Therefore, I assessed the influence of key life-history and ecological features (see Chapter 2, Table 1) on the variation in annual reproductive performance across all nesting stages in 65 bird species. The findings of this study demonstrate that differences in the number of eggs laid and in the proportion of eggs that survive until fledging are explained by different factors. Accordingly, I advocate that investigations of the evolution of reproductive strategies should consider selection pressures over the entire breeding cycle, and that reproductive performance only be compounded once the full reproductive effort has been invested.

In Chapter 3, I use a comparative experimental approach to investigate how avian parents differentially adapt their initial reproductive allocation when faced with adverse conditions for raising offspring, and the downstream effects of these early decisions on breeding success. Offspring predation is the primary source of reproductive failure for most bird species (Ricklefs 1969) and the mere fear of offspring predation can shape the evolution of reproductive decisions (Lima 2009). Yet, the influence of changes in risk to prospective offspring on reproductive decisions in ecological time remains unclear (Ibáñez-Álamo et al. 2015). Furthermore, most

previous experimental studies increased the perceived predation risk throughout the breeding cycle (Zanette et al. 2011, Hua et al. 2014, LaManna and Martin 2016). However, natural predation risk is ubiquitously irregular and responses can depend on the frequency and duration of high-risk situations (Lima and Bednekoff 1999, Ferrari et al. 2009). It has not been previously tested if risk of nest predation that is only perceived to be high prior to a reproductive attempt has downstream effects on reproductive success.

To investigate these questions, I temporarily increased the perceived risk of nest predation prior to egg-laying in 8 bird species and assessed life-history and ecological correlates of the subsequent reproductive allocation and success. This study corroborates that fear of offspring predation is an important factor influencing reproductive decisions and can have delayed consequences on fitness. In addition, I identify a novel mechanism for parents to adjust their reproductive allocation to the prevailing nest predation risk: species with a long parent-offspring association increased the variance of egg size within their clutch.

In Chapter 4, I focus on the reproductive decisions and performance of a long-lived species, the Siberian jay, using a combination of a longitudinal and an experimental approach (Griesser et al. 2017). Comparative work in mammals has demonstrated that long-lived species express low variance in survival but high variance in reproductive allocation, while the reversed pattern is found in short-lived species (Hamel et. al 2010, Fig. 1). We tested this prediction using long-term data to examine breeding decisions across years of varying quality in Siberian jays. We then experimentally tested the prediction by carrying out an experimental challenge with a novel pathogen before egg-laying, to induce a reduced breeding condition of females prior to breeding, in two years with contrasting weather conditions. We examine effects on initial reproductive allocation, adult survival, and offspring survival, an important contributor to fitness that is rarely investigated in this context. The findings of this study demonstrate that variable reproductive allocation is associated with a consistently low variance of adult survival, supporting patterns found in mammals (Gaillard et al. 1998). Moreover, they highlight that the temporal variance of a female's reproductive allocation can differ between its different stages, requiring the use of equivalent stages in comparative analyses.

In Chapter 5, I return to a comparative experimental approach, this time focusing on parental care decisions during provisioning of nestlings. Caring for offspring is costly, and biparental care relies on cooperation between parents to ensure the survival of their offspring, but is also a source of conflict. Both parents face a trade-off between current and future reproduction and should strive to reduce their own effort, in balance with their partner's effort, to ensure that offspring receive enough total care to survive while lessening current costs of parental care for themselves (Trivers 1972, Drent and Daan 1980). A pioneering model suggested that if one parent reduces its effort, its partner should partially compensate, with the increased costs distributed between the partner and the offspring (Houston and Davies 1985). Recent models have predicted that negotiation between the parents could lead to partial, full or no compensation by partners, depending on the costs and benefits associated with care (Jones et al. 2002, Johnstone and Hinde 2006). This negotiation process has been suggested to be influenced by several species traits, such as brood size, developmental mode and lifespan (Silver et al. 1985, Kokko and Jennions 2003, Olson et al. 2008). However, experimental tests of these ideas are lacking.

In this chapter I examine sources of variation in responses to an experimentally increased cost of caring for offspring by handicapping one parent of biparental pairs in five bird species. The results corroborate theoretical models which predict that negotiation over parental care can have different outcomes depending on the costs and benefits associated with caring. Species with high demands of parental care particularly shunted increased costs of care to their offspring, highlighting that greater attention should be paid to intergenerational trade-offs, particularly in species with a large obligation to parental care. Moreover, the results shed new light on life-history trade-offs, indicating that parental decisions may be weighed more against the current demands of a reproductive event than against the prospects of future reproduction.

1.3 Study Systems and General Methods

Study sites and species

Data for the experimental studies described in this thesis were obtained at several study sites. The comparative experimental work was primarily carried out at two sites in southern Spain. The Hoya de Guadix (37°25'N, 3°05'W) is characterized by a plateau of semi-arid scrublands cut by ravines and badlands, interspersed with Holm oak forests and dehesas (managed agro-silvo-pastoral lands common in the southern Iberian Peninsula). The study area in the greater Cordoba region (37°95'N, 4°40'W) is composed primarily of Holm oak forests and dehesas. Additional work was carried out in orange groves of the Lecrín region of Granada, Spain (36º 56' N, 3º 33' W) and in boreal forests near Arvidsjaur in Northern Sweden (65°40'N, 19°7'E). In total, data is reported for ten species across these field sites (Figure 3). The data analyzed in Chapter 2 come from published studies which have been conducted around the world.

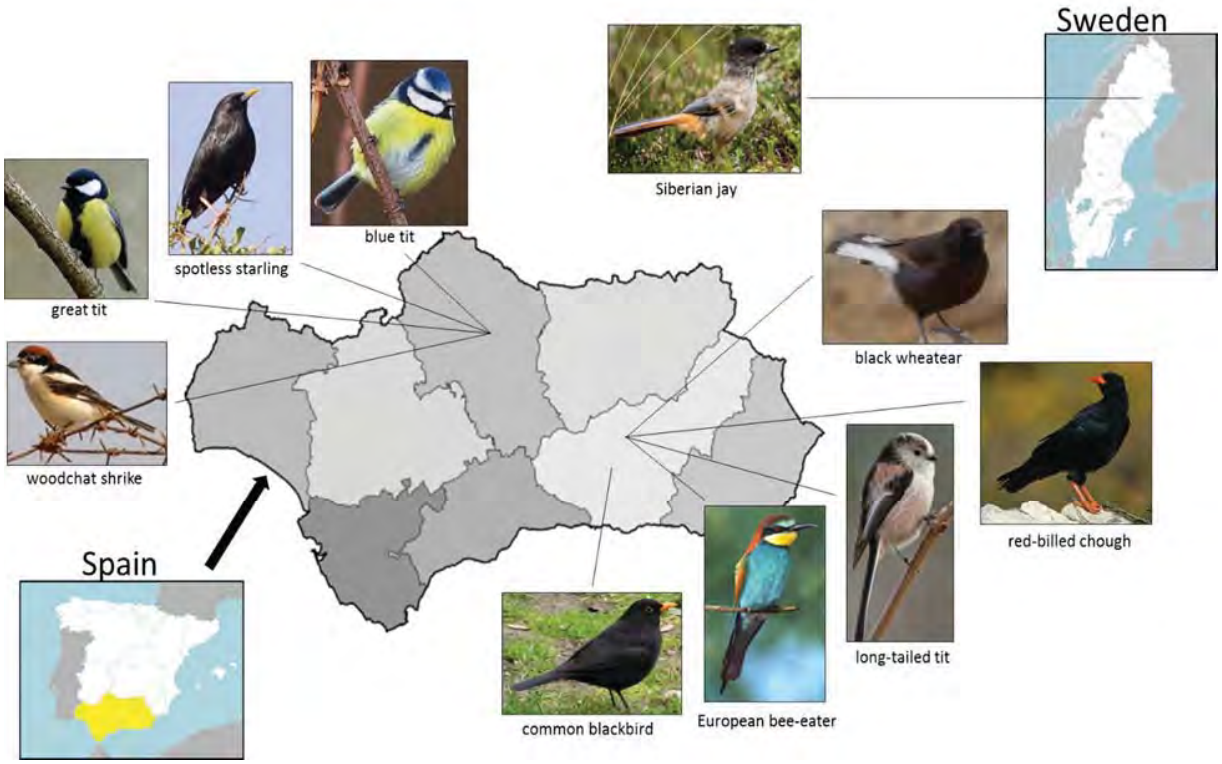

Figure 3: Field study locations and species

The study species with which I conducted experiments represent diverse traits along the life-history spectrum, ranging in body sizes, annual reproductive rates, and adult survival. In addition, these species face diverse risks during breeding, as they employ different nesting strategies and face distinct predation pressure and resource requirements. See Table 1 for an overview of the species studied.

Table 1: Study species differ in life history and ecology. 'Time in nest' is the average number of days from onset of egg laying until fledging, 'post-fledging time' is the average number of days spent in association with parents after fledging.

common name	scientific name	body [1] mass (g)	adult [2] survival (%)	nest [3] type	no. [2] broods	mean[1] clutch size	time [1] in nest (d)	time [2] post-fledging (d)	nest [1] predation rate (%)
Black wheatear	*Oenanthe leucura*	36	49.5	closed	2.5	4.0	31	200	26.8
Blue tit	*Cyanistes caeruleus*	9	41.6	closed	1.0	7.0	33	18	11.5
Common blackbird	*Turdus merula*	94	56.0	open	2.5	2.9	27	21	23.6
European bee-eater	*Merops apiaster*	52	49.8	closed	1.0	5.7	57	250	23.7
Great tit	*Parus major*	17	48.6	closed	1.5	7.5	37	30	28.2
Long-tailed tit	*Aegithalos caudatus*	7	55.0	open	1.0	7.3	32	300	49.4
Red-billed chough	*Pyrrhocorax pyrrhocorax*	310	80.0	closed	1.0	4.7	56	42	17.6
Siberian jay	*Perisoreus infaustus*	84	69.0	open	1.0	3.9	42	400	15.6
Spotless starling	*Sturnus unicolor*	74	49.9	closed	2.0	4.6	34	7	21.0
Woodchat shrike	*Lanius senator*	29	54.0	open	2.0	4.9	33	42	36.8

[1] Values obtained from the study population
[2] Values obtained from published data (e.g., del Hoyo et al. 2016)
[3] The long tailed tit's domed nest is here classified as an open nest, as it is functionally more similar to open nests than closed cavity nests.

General methods

The field work for this thesis involved monitoring several populations of birds (Table 1). Each study site was visited at the start of the breeding season for the respective populations (typically February or March). Adult individuals in each population were captured using mistnets or ground traps, and individually marked with a numbered aluminum ring as well as a unique combination of three colored plastic rings (Figure 3a). Because European bee-eaters have short tarsi, it is not possible to place multiple colored rings on them. Instead, we applied a non-toxic paint to either their outermost or central tail feathers for individual identification (Figure 3b). The drawback of this method is that the tail feathers are molted at the end of each breeding season, and thus it was necessary to recapture adults for marking each spring.

Fig. 3: (A) A color-ringed woodchat shrike and a (B) European bee-eater with painted central tail feathers feed their nestlings.

In 2010, we mounted nest boxes in the Cordoba study area, which were subsequently occupied primarily by blue tits, great tits, and spotless starlings. Each breeding season, once adults began to exhibit nesting behavior, we would thoroughly search for natural nests using behavioral cues and systematic searching, and begin to monitor nest boxes by checking for nesting activity every 2-3 days. Breeding behavior was then recorded throughout the season, including (when available): the dates corresponding to the onset of nest-building, egg-laying, hatching and fledging; clutch

size; egg dimensions; brood size; and sources of nest failure. Nests were often video recorded for the purpose of experiments (e.g., Chapter 5), using camcorders or infrared cameras. When nestlings reached an appropriate age/size, they were fit with aluminum and colored rings as per the adults. In addition, the tarsus, wing, and bill lengths; body mass; and number of fault bars on the wing and tail feathers were recorded. A small blood sample and feather sample was collected from each nestling. In addition to these general methods, each experiment conducted in the field followed its own protocol, which can be found in the respective chapters of this thesis.

All field studies ran in accordance with local regulations. Studies in Spain were conducted under licenses from the Junta de Andalucía and the Bird Migration Center (CMA) of the Spanish Ornithological Society (SEO), and Siberian jay experiments were conducted under licenses from the Umeå ethics board.

1.4 General Results and Discussion

Life history theory asserts that individuals face trade-offs which affect the allocation of resources into reproduction and between the stages of reproduction (Williams 1966, Stearns 1976). The results of the studies presented in this dissertation shed new light on the nature of life history trade-offs, and how these trade-offs interact with environmental factors to influence reproductive decisions and productivity in birds. Overall, my findings demonstrate that costs of reproduction can be mitigated through condition-dependent reproductive allocation. Flexibility of reproductive allocation primarily depended on the level of demand from offspring rather than life history pace. These findings highlight (i) the need to assess productivity independently at each reproductive stage, with more attention to reproductive output than initial allocation, (ii) that birds vary greatly in their responses to adverse breeding conditions, but that life-history pace may play a smaller role in this variation than previously believed.

Classic models of life history suggest that the interplay between life-history traits, the environment, and reproductive performance is direct, such that the environment and life-history traits dictate reproductive performance (which feeds back on each), and the environment further affects life history traits through phenotypic plasticity (Fig. 2). However, the results presented in

chapters 3-5 demonstrate that the breeding environment both directly (through ecological constraints) and indirectly (through phenotypic plasticity) affects reproductive performance in birds (Fig. 4). I predicted that life history traits themselves would feed into this relationship, by shaping a species' propensity for plasticity, yet life history played a minor role in predicting reaction norms among species (Chapters 3 and 5), and rather only contributed to mean fecundity (Chapter 2).

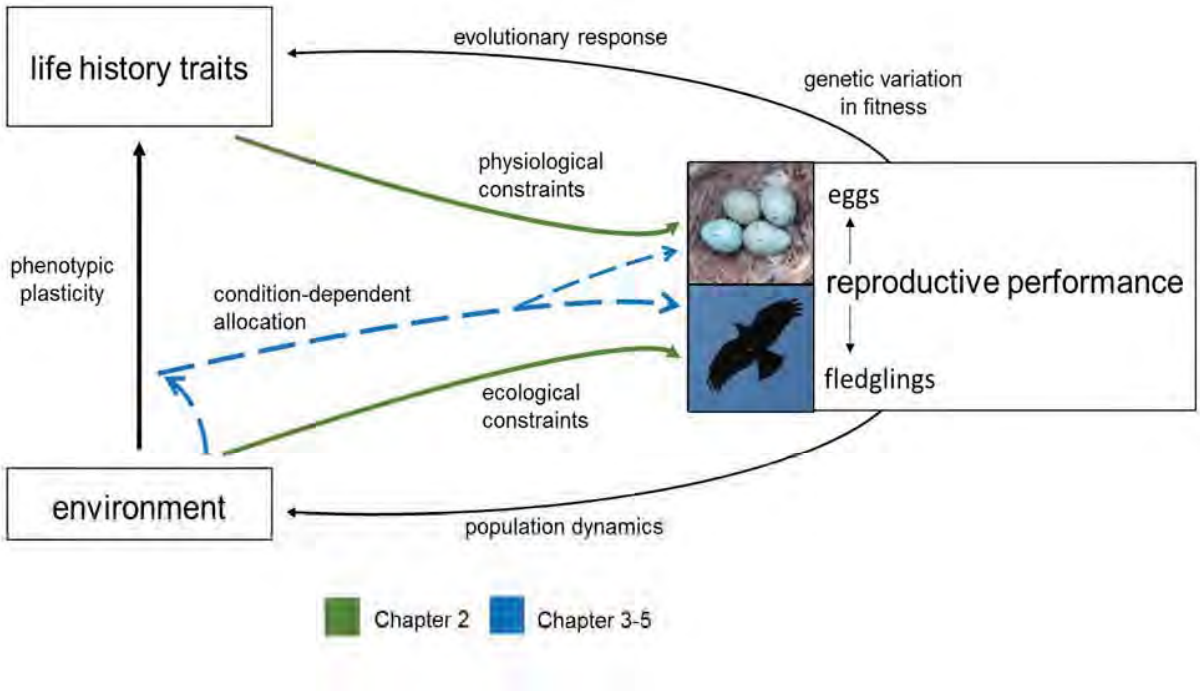

Fig. 4 Synthesis of thesis results. Reproductive performance is composed of multiple stages. The findings from Chapter 2 indicate that although life history traits determine the number of eggs, the environment dictates reproductive success. Chapters 3-5 reveal some ways that the environment indirectly affects reproductive performance through condition-dependent investment at different stages of reproduction. Solid lines denote associations predicted by the original paradigm (adapted from Ricklefs 2000), dashed lines indicate secondary relationships explored in this thesis.

Trade-offs between nesting stages

The findings from the comparative study reported in Chapter 2 confirm that interspecific variation in annual fecundity correlates with key intrinsic species traits (life-history pace, developmental mode, and migratory habits), but demonstrate that these traits are not related to realized reproductive success. Rather, the breeding ecology of a species (i.e., latitude, nest predation and habitat specialization) determines success at each stage of nesting, suggesting that offspring success is largely independent of, and has different constraints than, annual fecundity. Namely, at the population level, physiological constraints limit the number of eggs laid, but ecological constraints limit the realized number of offspring (Figure 4).

Natural selection acts on successful offspring, thus the findings from these comparative analyses emphasize that studies investigating measures of fitness and the evolution of reproductive strategies should focus on the selective pressures throughout an entire breeding cycle and reproductive performance be compounded once the full effort has been invested. Contrary to our expectations, success at either stage of nesting (and overall) was unrelated to annual fecundity, despite a high variance of success across species. Therefore, species with particularly small, or particularly large, annual number of eggs did not have greater reproductive performance relative to their investment. This result demonstrates that clutch size is not directly mediated by the probability of offspring survival to independence, nor vice versa. Thus, females may not be able to regulate clutch size according to offspring rearing conditions (Erikstad et al. 1998). Inconsistent results regarding the effects of clutch size manipulations on fitness components within species (Dijkstra et al. 1990) reinforce this finding. Alternatively, examining only mean values of allocation across individuals may dilute important processes of individual variation, whereby each individual suitably monitors their own breeding condition but the benefits are not apparent at the population level. Nevertheless, my results emphasize that fecundity relates to breeding success differentially across species and thus inferences of fitness based on numbers of eggs, especially in comparative studies, may be of limited usefulness and should be approached with care.

Phenotypic plasticity and mitigation of reproductive costs

Although the findings from the comparative study in Chapter 2 suggest that, at the population level, reproductive performance does not relate to initial allocation, there is evidence that individual plasticity (i.e., flexible reaction norms) can be adaptive under varying environmental conditions in ecological time (Ghalambor et al. 2007). Phenotypic plasticity is considered adaptive if it allows individuals to achieve higher fitness by adjusting to their environment than they would if they remained constant, despite its inherent costs. However, the fitness benefits of plasticity can be limited by the predictability and reliability of environmental cues (Reed et al. 2010), and therefore can relate to life history traits in important ways. For example, long-lived mammals (i.e., species with a maximum lifespan above the mean: 16.4 years, Jones et al. 2009) require 3.5 times longer than long-lived birds (i.e., species with a maximum lifespan above the mean: 15.7 years, Valcu et al. 2014) to raise their offspring from conception to independence (404 vs.117 days). Therefore, in comparison to long-lived mammals, birds of similar lifespan may be in a better position to predict the conditions that they will experience while rearing offspring and match their reproductive allocation accordingly, affecting the evolution of reproductive allocation strategies.

In Chapters 3, 4, and 5, I explore how the reaction norms to breeding challenges differ among and within species, and examine potential causes and consequences of reproductive flexibility. Overall, the findings indicate that birds vary widely in their reaction norms, and the degree of flexibility may depend more on the demands of raising current offspring than on the prospects of future reproduction. Furthermore, the data presented in this dissertation suggest that individuals regulate costs of reproduction by adjusting the number of eggs, and/or the effort invested into caring for offspring, depending on the breeding conditions.

A temporarily increased nest predation risk prior to egg-laying (Chapter 3) has detrimental downstream effects on reproductive success. In general, birds decreased their clutch volume when faced with an increased risk, which was a combined effect of minor reductions to clutch size and egg volume. The results additionally show, for the first time, that birds may respond to a high risk of nest predation by altering the distribution of their reproductive allocation across their eggs, resulting in a marked increase in within-clutch variation of egg volume. This response predictably

varied with prolonged parent-offspring association but did not differ along a life-history spectrum (as measured by a principal component of body mass, developmental time, and adult survival). This novel link between within-clutch egg size variation and perceived predation risk highlights that family-living species (Drobniak et al. 2015, see Appendix) may be particularly inclined to employ a bet-hedging strategy under unpredictable, high risk conditions. Such a strategy may be most effective in those species with ample opportunity to compensate for poor offspring quality post-fledging, when the risk of losing the entire brood is considerably reduced.

Long-term data from Siberian jays (Chapter 4) reveal that females produce fewer eggs and fledglings in unfavorable years, yet offspring quality does not vary between years or individuals, nor does the survival of fledged offspring or females. Similar to patterns found in long-lived mammals (Hamel et al. 2010), the temporal variance of reproductive performance is larger than the variance of adult survival. An experimental challenge with a novel pathogen supports these patterns, even to the extent that females with an experimentally reduced body condition elected to skip breeding in a bad year. Furthermore, immune-challenged Siberian jays that initiated a nest in the unfavorable year seemed to offset down-stream costs to themselves by abandoning their nests early on, suggesting that they assessed costs of reproduction continuously.

Across five species, an increased cost of parental care at the nestling stage (Chapter 5) generally resulted in reduced care by the parent incurring higher costs, and the additional costs were shared by the partner and their offspring. This effect was mediated by the length of time that the offspring require parental care. Species with a long duration of parental care primarily shunt increased costs to their offspring, while care is compensated by the partner in species with a short duration of care. Surprisingly, life history pace (i.e., adult survival and fecundity) did not influence parental decisions when faced with a higher cost of caring, even though life-history theory predicts long lived species to be most sensitive to adverse breeding conditions (Charlesworth 1994).

The combined findings of the studies presented in this dissertation highlight that the degree to which avian parents can, or will, adjust their reproductive allocation differs greatly. Plasticity of reproductive allocation primarily depended on the level of demand from offspring rather than life history pace. Contrary to life history theory (Williams 1966, Roff 1993), these findings suggest that

species across the life history spectrum may allocate similar proportions of energy to survival (see also Santos and Nakagawa 2012). Therefore, while life history sets the upper limit for the number of offspring a given species can reasonably care for in a reproductive event, the current conditions (both the state of the environment and the physical condition of the parents) determine the achieved fitness of individuals within the range tolerated by that species' life history. Species with long parental care periods emerged as the most sensitive to adverse conditions, regardless of survival prospects. Furthermore, across these studies, I found that the phenotypic plasticity in reproductive decisions increasingly affected the success of offspring along the nest stages. As the costs of reproduction accumulate over a breeding cycle, it is not surprising that mechanisms for counteracting these costs accumulate as well.

1.6 Outlook

The results presented in this dissertation lay a foundation for novel avenues of future research. Longitudinal repeated measures of reproductive behavior from several populations of birds provide an outstanding resource for continuing in-depth comparative studies of patterns of reproductive decisions, life-history trade-offs, and reaction norms across species. In ongoing projects, we are validating our findings and expanding our questions. For example, one project in progress is focused on inter-annual variation in reproductive parameters relative to the predictability of the environment, using the same large-scale dataset presented in Chapter 2 in conjunction with detailed climatic data from each study location.

We have also conducted additional experiments at our study sites in Spain, which are currently being processed. For instance, two separate comparative experiments investigate plasticity in incubation and nestling provisioning behavior when parents face risks to themselves and to their offspring. Preliminary results from these studies indicate that, independent of life history, birds are more concerned about their own survival than the survival of their offspring. Another experiment examines the costs associated with delayed dispersal after independence in a species with prolonged offspring retention, and suggests that the benefits of group living over winter explain offspring retention more than benefits of staying with parents *per se*.

Several notable questions arose from the results presented here. In light of the findings presented in Chapter 3, it would be interesting to test how an increased variance in allocation across offspring, rather than total allocation, in the face of predation risk affects productivity when conditions remain unfavorable as opposed to improving over the nesting cycle. Additionally, because an increased nest predation risk only at the time of egg-laying had delayed detrimental effects on reproductive success, it would be useful to assess how variable risk levels at different times during the breeding cycle ultimately affect reproductive success. Finally, responses to nest predation risk prior to breeding are clearly not "one size fits all" among species, accentuating the need for additional comparative studies to understand the evolved mechanisms for coping with changes to offspring predation risk and to develop a framework of how other life-history, ecological and/or social factors contribute to interspecific differences.

The results from Chapter 4 highlight the need for further investigation in bird species with diverse life history strategies, to determine if the production of consistent offspring quality, independent of environmental or female body condition, is a general trend among long-lived bird species. Furthermore, because offspring quality has been shown to have downstream fitness effects (Lock 2012, Burton and Metcalfe 2014), future life-history models on reproductive allocation should consider the variance of reproductive allocation (i.e., number of eggs or litter size), reproductive output (i.e., number of fledglings or weaned offspring), and offspring quality and survival. Siberian jays exhibited a low variance of initial reproductive allocation as well as female and offspring survival, with a high variance in fledging success, but the patterns of variance in these traits across all birds are currently unknown, and would be an interesting path for future investigation.

Finally, the findings of the handicapping experiment reported in Chapter 5 highlight that greater attention needs be paid to intergenerational trade-offs, particularly in species with long developmental (and thus parental care) periods. Most studies of the costs of parental care focus on the trade-off between current and future reproduction or survival (intraindividual trade-offs, e.g., Owens and Bennett 1994, Webb et al. 2002, Alonso-Alvarez and Velando 2012, Santos and Nakagawa 2012), while relatively few studies have addressed the fitness consequences of parental decisions on current offspring (intergenerational trade-off, as discussed in Stearns 1989).

Furthermore, we were unable to robustly test sex differences in responses. However, the available data indicated that both sexes reduced their care when handicapped, but that unmanipulated males may be more likely to compensate for a reduction of care by their partners than unmanipulated females. If so, this may be because females are already providing care at their maximum capacity (MacGregor and Cockburn 2002, Low et al. 2012) and may be more likely to transfer costs of reproduction on to their offspring than males (Santos and Nakagawa 2012). Further work should be done to confirm the patterns observed in our data.

Flexibility in a changing world

The concept that individuals can adaptively adjust their behavior and allocation of resources to competing demands is a foundation of behavioral ecology (Krebs and Davies 2009). However, the natural world is currently changing at an unprecedented pace and scale (Chevin et al. 2010). Human activities in particular are having a profound impact on ecosystems worldwide. Issues such as climate change, habitat destruction, overharvesting and the spread of invasive species are confronting species with rapidly and extensively changing environmental conditions which they have not experienced in their evolutionary history (Vitousek et al. 1997, Walther et al. 2002, Parmesan and Yohe 2003). Phenotypic plasticity provides a potential mechanism for organisms to deal with temporal and spatial environmental variation (Canale and Henry 2010) and a growing body of research is beginning to demonstrate that behavioral flexibility plays an important role in responses to change, at least partially explaining why some species to flourish while others struggle in today's world (Tuomainen and Candolin 2011, Sih 2013, Snell-Rood 2013). However, investigations of phenotypic flexibility during reproduction are relatively scarce (Vézina and Salvante 2010), and a broad understanding of how and why flexibility in reproductive traits varies among species remains elusive. Given the importance of reproductive traits to population fluctuations and conservation measures, it is surprising that the causes and consequences of reproductive flexibility have received so little attention.

Generally, organisms can respond to adverse changes in their environment through three strategies: dispersal, adaptive genetic change, and phenotypic plasticity (Wong and Candolin 2015). Considering the current rates of environmental change, plasticity may arise as the first line

of defense for many animals. Opportunities for dispersal may be limited due to ongoing habitat destruction and fragmentation. Similarly, evolutionary processes may not be able to keep up with the current rates of environmental changes, particularly in species with a slow pace of life (Chevin et al. 2010, van Schaik 2013, Vedder et al. 2013). One meta-analysis (Hendry et al. 2008) demonstrated that phenotypic changes are generally greater in anthropogenic contexts than under natural environmental variation, and that such changes are chiefly due to phenotypic plasticity rather than genetic evolution. As the world becomes increasingly dominated by humans, it will be crucial to understand whether and how organisms cope with these changes.

The results presented in this dissertation highlight that species vary in the strength of their responses to heterogeneity in breeding conditions and reveal some potential causes of that variation. Further work is needed to expand our knowledge of how behavioral flexibility influences evolutionary responses of organisms to environmental change and what circumstances might facilitate, or impede, adaptation. Furthermore, it is important to determine how changes in behavior will result in feedback loops which mediate evolutionary and ecological processes. Improved knowledge of these pathways will be crucial to projecting the prospects for species in the long term and, where possible, to counteract the loss of biodiversity.

Chapter 2

Selection over the reproductive cycle: intrinsic factors determine initial reproductive allocation, environmental factors determine breeding success in birds

Gretchen F. Wagner [1], Szymon M. Drobniak[1,2], Michael Griesser[1]

[1] Department of Anthropology, University of Zürich, Zürich, Switzerland
[2] Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland

Chapter 2

2.1 Abstract

Reproductive allocation varies greatly across species and is determined by their life-history and ecology. While many studies only assess variation in allocation early in a reproductive cycle, reproductive success is a better fitness proxy than fecundity (i.e., the number of eggs or propagules). Thus, it may be critical to look beyond fecundity to understand the evolution of life-histories and how life history components interact with each other. Here we assessed the influence of species traits and ecology on the variation in reproductive performance across all nesting stages in 65 bird species. Phylogenetic-controlled models revealed that sedentary species and those with a fast life-history pace had the highest annual fecundity, supporting findings from earlier studies. However, the annual breeding success (i.e., the proportion of eggs which yield fledged offspring) was highest in species that breed at high latitudes, have low nest predation rates, and are habitat specialists. Breeding success was unrelated to annual fecundity, demonstrating that females may not be able to regulate their initial allocation according to future breeding conditions. Moreover, this result emphasizes that measures of fecundity relate differently to breeding success among species and thus inferences of fitness based on numbers of eggs in comparative studies may be equivocal. We advocate that studies investigating the evolution of reproductive strategies should focus on the selective pressures throughout the breeding cycle and reproductive performance only be compounded once the full reproductive effort has been invested.

2.2 Introduction

Life history theory provides a framework to understand interspecific variation in reproductive allocation. The central concept of life history theory is that individuals have limited resources to allocate among growth, survival and reproduction (Williams 1966, Stearns 1992). Species with a slow pace of life are expected to minimize the costs of a reproductive event in favor of survival and future reproduction, while those with a fast pace of life are expected to allocate more energy into current reproduction, potentially at the expense of their own survival. However, life history traits alone do not fully explain variation in reproductive performance among species. Empirical studies have shown that reproductive allocation is often modulated by environmental factors, such as predation risk to offspring or resource abundance (White 2008, Sofaer et al. 2012).

Theoretical work has made great strides in predicting optimal reproductive allocation under diverse conditions and life-history trajectories across organisms and lineages (e.g., Schaffer 1974, Kozłowski 1992, Brommer 2000). Yet, broad empirical comparisons to test these theories are hindered by focusing on non-analogous traits in different taxa. In many organisms, reproductive productivity is measured at the end of parental investment (e.g., the yield of seeds in plants (Shaanker et al. 1988) or the number of offspring successfully weaned in mammals (Hamel et al. 2010)). Clearly, these measures are a better fitness proxy than the numbers of ovules or offspring born and reflect the total amount of reproductive effort that has been allocated to them. Egg-laying organisms that lack parental care (e.g., many reptiles, amphibians, fish and insects) are most analogous to plants in their breeding cycle, as their reproductive effort is complete after oviposition (Wiens 1984). However, nearly all birds and numerous other egg-laying organisms require continued parental effort after egg-laying. Yet it is common to measure reproductive productivity in these animals as the number of eggs (e.g., Elgar 1990, Jetz et al. 2008, Gilbert and Manica 2010), which ignores the parental effort dedicated to raising offspring and the ecological factors that strongly influence reproductive success. As reproductive success drives natural selection, it is critical to look beyond the initial stages of reproductive allocation to understand the evolution of life-histories and how life history traits interact with each other.

Table 1 Demonstrated relationships between reproductive traits and life history/ecological factors in birds.

Reproductive Trait	Variable	Relationship	Studies
clutch size	lifespan (survival)	short > long	1-4
	developmental mode	precocial > altricial	5, 6
	body mass	small > large	5-7
	migration	sedentary > migratory	6, 8, 9
	absolute latitude	high > low	5, 10-12
	nest predation	rare > frequent	2, 13, 14
	nest type	closed > open	2, 5, 6
annual fecundity	lifespan (survival)	short > long	1, 2
	developmental mode	precocial > altricial	6, 15
	body mass	small > large	6
	migration	sedentary > migratory	2, 6
	absolute latitude	none	6
	nest predation	frequent>rare	2
	nest type	closed > open	6, 13
	social system	prompt dispersal > prolonged parent-offspring association	16
hatching success	nest predation	rare > frequent	17
	absolute latitude	high > low	18
	nest type	closed > open	19
	social system	non-cooperative breeding > cooperative breeding	20
breeding success	nest type	closed > open	19

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Studies of clutch size in birds have been a foundation for the study of life history evolution in general (Martin 2004, Jetz et al. 2008). However, individuals not only trade-off the amount of energy allocated into reproduction but also the distribution of that energy into each component of reproduction (Winkler and Walters 1983, Martin 2004), such as egg production, incubation and offspring provisioning. Although the clutch size sets the upper limit for the number of successful offspring in a reproductive attempt, it may not reflect actual differences in reproductive success due to variation in the number of clutches or in the success of raising offspring to fledging (Murray Jr 2000, Etterson et al. 2011). Within the tropics, for example, most birds have minimal variation in clutch size from a mode of 2, but a wide variation in nesting success (Skutch 1985, Martin 1996, Robinson et al. 2000). Yet, theory predicts that clutch size trades-off with the probability of juvenile survival to independence (Lack 1947, Morris 1987, Mangel et al. 1994).

Both intrinsic traits and extrinsic factors have been suggested to influence clutch size (see Table 1). For example, long-lived species (which tend to also be large-bodied (Speakman 2005)) prioritize survival over current reproduction and accordingly have smaller clutches than smaller, shorter-lived species, and altricial species offset higher demands of parental care by laying less eggs than precocial species. A few studies have moved beyond clutch size to incorporate the number of clutches into measures of annual fecundity (the number of eggs laid in a year), showing that the same factors which explain differences in clutch size can have no or opposing effects on annual fecundity (Table 1). Species living at low latitudes have smaller clutch sizes, but tend to lay more clutches, resulting in similar annual fecundity among latitudes (Böhning-Gaese et al. 2000). Nest predation pressure is negatively correlated with clutch size but positively correlated with annual fecundity (Martin 1995). This suggests that birds counteract high nest predation risk by spreading their reproductive allocation among multiple clutches rather than putting all of their eggs “in one basket”. Considering that selection acts on individual breeders, not nests or eggs, measures of annual productivity are more pertinent to demographic and evolutionary studies than those of single reproductive events, yet they are relatively uncommon in avian studies.

There have been numerous calls to extend measures of fitness in birds beyond the number of eggs (Martin 2004, Anders and Marshall 2005, Etterson et al. 2011), yet few studies have examined

sources of interspecific variation in the survival of eggs or dependent offspring. Those which have (see Table 1) have been limited in their scope and only one (Spottiswoode and Møller 2004) controlled for phylogenetic non-independence among species. Furthermore, to our knowledge, no comparative test of the factors which affect reproductive investment differentially across nest stages has previously been carried out. Field studies of individual species have demonstrated that individuals can trade-off their reproductive effort between stages (Heaney and Monaghan 1996, Monaghan et al. 1998, Russell et al. 2007), reinforcing the view that the level of investment at one reproductive stage does not necessarily translate into reproductive success (Murray Jr 2000). Furthermore, a comparative study indicated that clutch size is positively related to parental energy expenditure and length of the nestling period, most likely driven by nestling predation risk (Martin et al. 2000). These results imply that the environmental and reproductive demands at later stages of nesting can feed-back to affect the evolution of clutch sizes (Morris 1987). Thus, a framework of how species traits and environmental factors influence trade-offs in reproductive allocation across nesting stages will help to understand the evolution of reproductive tactics and success among birds.

Following life history theory, we expect an inverse relationship between annual fecundity and nesting success (Morris 1987, Monaghan et al. 1998). We further hypothesize that the low fecundity of long-lived species will be balanced by a higher investment into parental care, resulting in a higher proportion of offspring survival to fledging. Species with specialized diet and habitat requirements and/or high nest predation pressure are expected to have higher annual fecundity to offset losses due to harsh or unpredictable environmental conditions. Finally, high costs of parental care are expected to foster low fecundity but high nesting success in species with altricial young and/or an extended association between parents and offspring ("family-living", Drobniak et al. 2015). However, in cooperative breeders, we expect higher fecundity as well as high nesting success, because helpers may reduce the costs of parental care. To test these hypotheses, we compared the factors which select for annual fecundity, the proportions of eggs and nestlings that survive until the following stage, and the proportion of eggs that fledge, in 68 populations of birds (N=65 species), controlling for phylogeny and the abovementioned correlates of fecundity.

2.3 Methods

Data Collection

We searched for long-term bird studies reporting mean numbers of eggs, nestlings and fledglings over multiple years (mean number of years: 8.05, range: 3-41 years) in a given location using online databases (N=67 species; 71 populations). In addition, we obtained data from nest card records (N=7 species; see Table S1 in Supplementary Material for complete data source list). We collected the following life history and ecological data for each species in our dataset (detailed definitions are given in the Supplementary Material): average lifespan, body mass, egg volume, developmental mode (precocial, altricial), social system (non-family living, family living, cooperative breeder; Drobniak et al. 2015), nest predation rate, nest type (open, closed), diet (generalist, specialist), habitat (generalist, specialist), latitude of the studied population, and migratory habits (migratory, sedentary). When available, this information was taken from the source from which we acquired the breeding data, otherwise it was obtained from handbooks (Maclean and Robert 1985, Cramp et al. 1994, Poole 2005, Higgins et al. 2007, Del Hoyo et al. 2011) or publications (see Supplementary Material).

We calculated the annual reproductive output of each population by multiplying the mean number of eggs, hatchlings, and fledglings each by the mean number of clutches per year. When annual numbers of clutches were not provided for a population, we classified them to the nearest 0.5 clutches according to reported species-level averages (following Martin 1995). As a measure of success at each nest stage, we calculated the proportion of eggs which hatched (hereafter called hatching success), the proportion of hatchlings which fledged (hereafter called fledging success), and the proportion of eggs which fledged (hereafter called breeding success) as a measure of overall success relative to initial allocation.

Statistical Analyses

We used a principal components analysis (PCA; package 'psych' (Revelle 2015)) to reduce the dimensionality of our original set of continuous predictors (lifespan, body mass, and nest predation rate), because many traits within a species are correlated (Stearns 1992). We relied on

the correlation matrix among variables to generate PCA scores rather than the covariance matrix (Graham 2003) because the units of measurement for traits differed. The inspection of a scree plot and eigenvalues (package 'nFactors' (Raiche 2010)) suggested the extraction of 2 components, cumulatively accounting for 76% (43 and 33%, respectively) of the total variance in the included variables (Table S2). The first component, labelled "life-history pace", included adult body mass and lifespan. High values of this component represent large-bodied, long-lived species. The second component, labelled "nest predation", included only nest predation rates. We tested for multicollinearity between explanatory variables by calculating the generalized variance inflation factors (GVIF; package 'car' (Fox and Weisberg 2011)) with the full set of predictors and each subset of predictors after model selection. GVIF values for all predictors were less than 2.5 in all cases.

We used MCMCglmm (Hadfield 2010) in R 3.1.0 (R Core Team 2014) to run phylogenetically controlled linear mixed models (LMM) on transformed (if necessary), scaled (to unit variance) and centered variables (Schielzeth 2010). Non-significant ($p<0.05$) fixed effect variables and their interactions were removed using a backward elimination procedure. We included in all models a maximum clade credibility supertree from recent phyla-wide phylogeny (Jetz et al. 2012). In all runs we have employed weakly informative priors for fixed effects (normal with large ($>10^6$) variance) and for variance components (inverse Wishart distribution for residual variance; parameter-expanded priors with large variance for other random effects; Hadfield 2014). Models were run for 200,000 iterations with a burn-in period of 25,000 iterations and thinning interval of 100 iterations. Proper mixing of MCMC chains was confirmed by reasonable (~1,000) effective sample sizes of posterior distribution samples for all estimated parameters and negligibly low autocorrelations (package 'coda' (Plummer et al. 2008)).

Each model was based on the subset of species for which the respective data were available. This restriction had an important consequence: while all studies included here reported mean annual fecundity, some studies failed to provide numbers for either hatchlings (N=7), fledglings (N=14) or both (N=6), thus reducing the data available for comparing across nest stages. Therefore, we do not report on the basic number of hatchlings or fledglings between species, as different subsets

of species would be represented within each model's results, limiting our ability to compare across stages. Instead, we report the ratios of values between stages (hatching success, fledging success, breeding success), as these models include the full set of species for which we have values of both stages in question and thus enable more robust comparisons. We first examined the effects of the explanatory variables and their interactions on annual fecundity. In addition, we tested egg investment in terms of body mass-adjusted annual productivity (following Sibly et al. 2012). These results (Table S3) were similar in direction and strength to annual fecundity. We then examined the relationship between the above-mentioned life history and ecological traits and hatching success, fledging success and breeding success. Finally, we tested whether each measure of success related to annual fecundity in separate linear mixed models, including the measure of success as a fixed term.

All analyses were based on species-typical attributes that were averaged across annual population-level observations. To facilitate interspecific comparisons, we averaged the data into single, species-specific values, with the advantage that the resultant values average annual reproductive parameters over several years. If within-population (intraspecific) variation in reproductive parameters and/or environmental factors differs drastically across years, intraspecific variation may bias observed patterns of interspecific variation, so we tested inter-annual variation in breeding parameters within the study populations. To achieve this, we have analyzed analogous models using respective (log-transformed) variances (inter-annual variance in annual fecundity/nestling numbers/fledgling numbers) as response variables, retaining the same set of fixed-effects (with the addition of respective means as fixed covariates).

2.4 Results

Interspecific variation in annual fecundity was best explained by life history pace, migration, developmental mode and an interaction between nest predation and developmental mode (Fig. 1a). Annual fecundity was inversely related to life history pace and migratory habits. Precocial species laid more eggs than altricial species, but the developmental mode interacted with nest predation rate, such that precocial species had a negative relationship with nest predation while there was no significant relationship for altricial species (Fig. 1b).

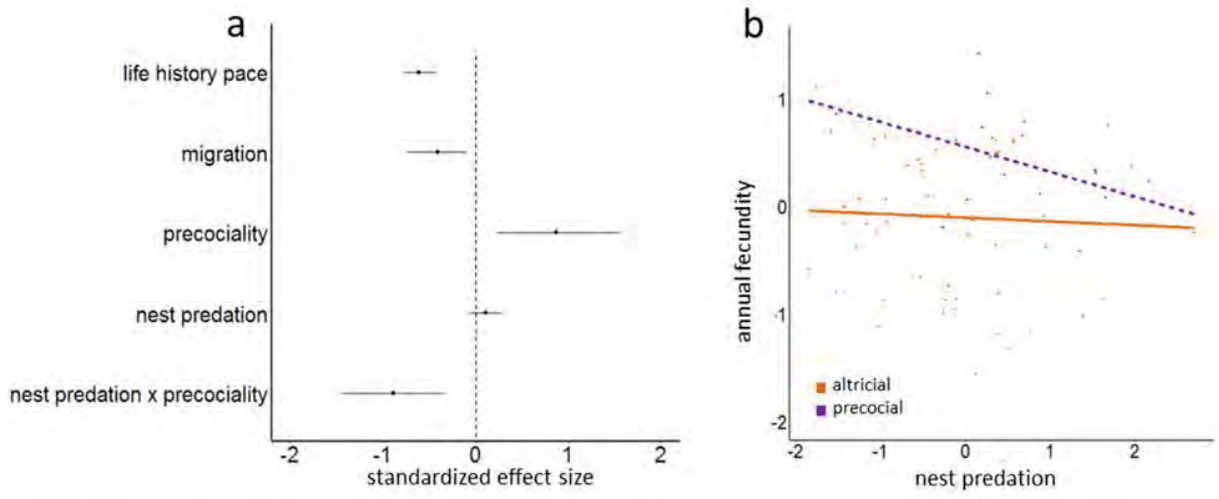

Fig. 1: Model results of annual fecundity: (a) Coefficient estimates and 95% credible intervals of the effect sizes for each of the significant predictor variables (scaled) (b) Model predictions of the relationship between annual fecundity, nest predation, and developmental mode, keeping the effects of other predictors constant.

Hatching success was 0.77±0.16 (mean±SD) across species. Variation in hatching success was best explained by nest predation, absolute latitude, and an interaction between life history pace and social system (Fig. 2a). Not surprisingly, hatching success decreased with increasing nest predation rates and species breeding at higher absolute latitudes had higher hatching success. Cooperatively breeding species had decreasing hatching success with a slow life history pace, while family living and pair breeding species showed no relationship between life history pace and hatching success (Fig. 2b). Fledging success (mean±SD = 0.72±0.22) depended on life history pace, nest predation,

absolute latitude, and habitat specialization (Fig. 3). Species breeding at high absolute latitudes and those with habitat specialization had greater fledging success, while high nest predation and slow life history pace was related to low fledging success. Breeding success (mean±SD = 0.56±0.21) was linked to the combined effects of nest predation, absolute latitude and habitat specialization (Fig. 4). Habitat specialists and those breeding at high absolute latitudes had higher breeding success, while species with high nest predation had lower breeding success.

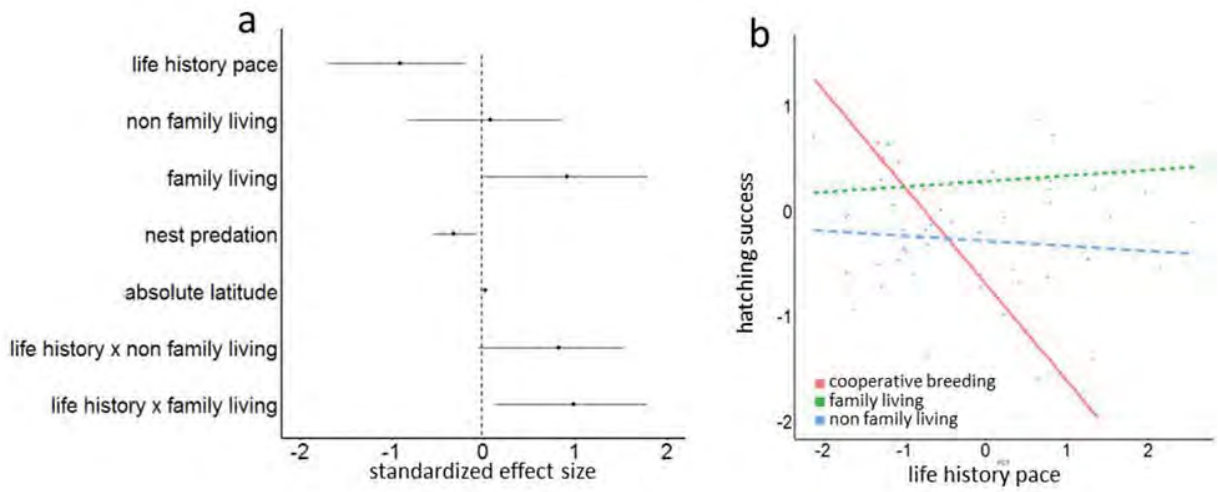

Fig. 2: Model results of hatching success: (a) Coefficient estimates and 95% credible intervals of the effect sizes for each of the significant predictor variables (scaled) (b) Model predictions of the relationship between hatching success, life history pace, and social system, keeping the effects of other predictors constant.

The mean annual fecundity was unrelated to hatching success (Estimate= -0.10, 95% CI= -0.39 – 0.19, pMCMC=0.54), fledging success (Estimate= -0.01, 95% CI= -0.39 – 0.41, pMCMC=0.96), and breeding success (Estimate= -0.06, 95% CI= -0.35 – -0.18, pMCMC=0.68). Between-year intraspecific variance in annual fecundity depended on nest type and latitude. The highest variance in annual fecundity was found in species breeding at low absolute latitudes (Estimate= -0.014, 95% CI= -0.024 – -0.003, pMCMC=0.018, Table S4) and open-nesting species (Fig. 5, Table S4). Open-nesting species also had higher between-year variance in the number of hatchlings (Fig. 5, Table S5) and number of fledglings (Fig. 5, Table S6).

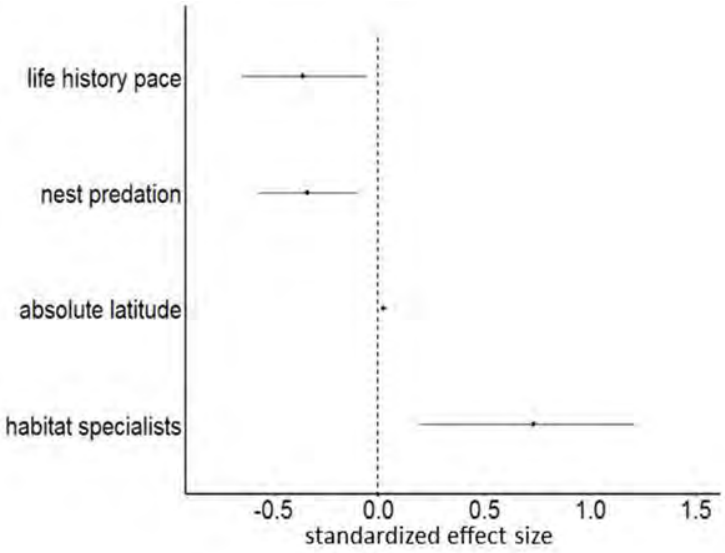

Fig. 3: Model results of fledgling success: Coefficients and 95% credible intervals for each of the significant predictor variables (scaled)

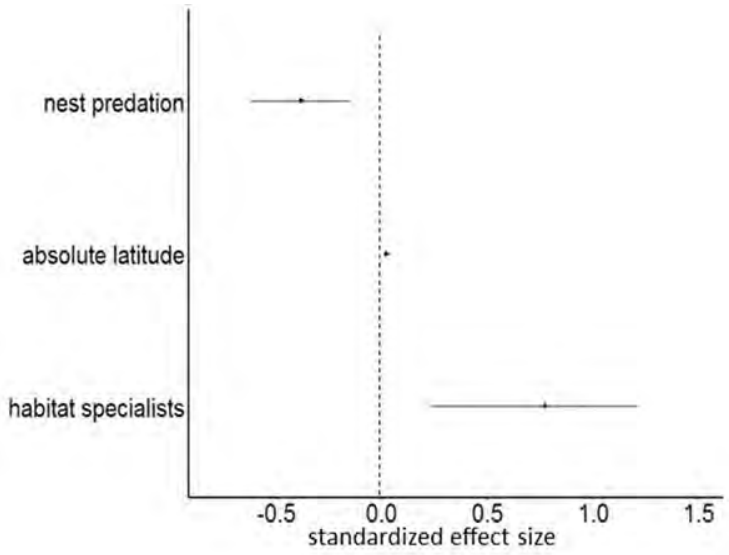

Fig. 4: Model results of breeding success: Coefficients and 95% credible intervals of the effect sizes on breeding success for each of the significant predictor variables (scaled).

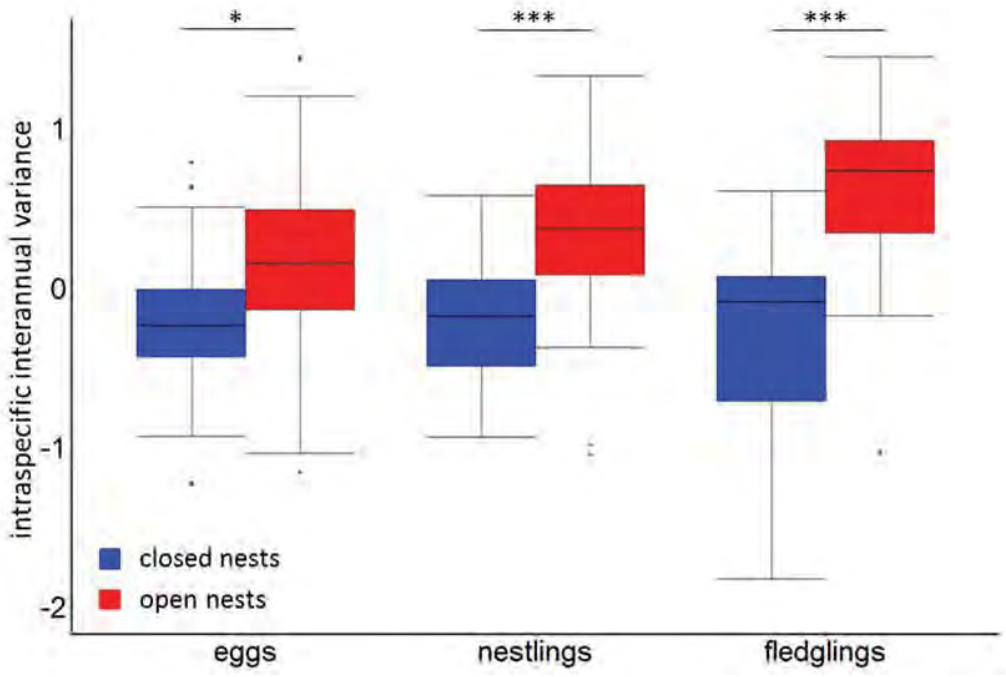

Fig. 5: Interannual variance across stages: Model predictions of the relationship between within-species between-year variance in number of offspring (log-transformed and scaled) and nest type at each nesting stage while controlling for phylogeny and mean numbers of offspring at each stage. *p=0.01, ***p<0.001

2.5 Discussion

Life history theory asserts that individuals face trade-offs which affect the allocation of resources into reproduction and between the stages of reproduction (Williams 1966, Stearns 1976). Our results confirm that variation in annual fecundity correlates with intrinsic traits of species (life-history pace, developmental mode, and migratory habits), and demonstrate that these traits are not related to reproductive performance (Fig. 6). Rather, traits related to the breeding ecology (i.e., latitude, nest predation and habitat specialization) determined success at each stage of nesting (Fig. 6). Our results suggest that reproductive success is independent of annual fecundity and has different constraints. Thus, our hypotheses for trade-offs in investment between nest stages did not hold true. Instead, our results demonstrate that the factors selecting for variation

in reproductive allocation vary among components of reproduction, highlighting the need to assess productivity independently at each reproductive stage or only once parental effort has completed.

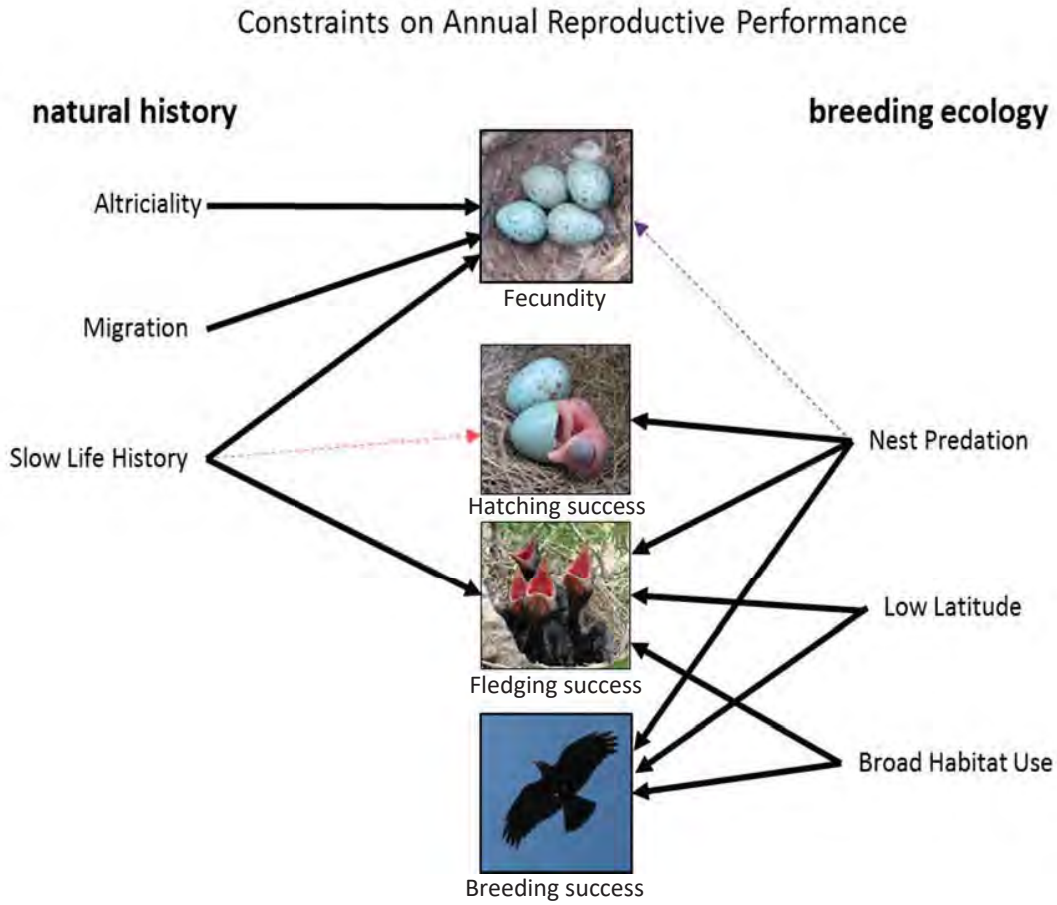

Fig. 6: Synthesis of factors constraining reproductive performance at each stage of nesting. Natural history traits are deep-rooted species characteristics, which largely inhibit reproductive performance through reduced annual fecundity. Breeding ecology factors comprise the species' interaction with the environment, and primarily reduce nesting success. Thick arrows represent direct relationships between the factor and reproductive performance; dashed arrows indicate interactions where the factor only effects breeding performance in precocial species (purple) or cooperative breeders (red).

Annual fecundity

Our analysis of annual fecundity confirms the findings of previous comparative avian studies, namely that life-history pace is a key factor influencing initial reproductive investment strategies (Zammuto 1986, Ricklefs 2000, Ghalambor and Martin 2001), and that migratory species are less

fecund than non-migratory species (Böhning-Gaese et al. 2000, Bruderer and Salewski 2009). We also found that birds likely trade-off parental care with fecundity (Jetz et al. 2008, Sibly et al. 2012), as evidenced by the high fecundity of precocial species, yet we found no relationship between fecundity and social system. While family living species have been previously shown to have lower annual fecundity than non-family living species (Drobniak et al. 2015), our results do not support this view. This difference may have arisen because we controlled for a number of other species traits, such as lifespan and developmental mode.

Nest predation rates only influenced annual fecundity among precocial species. This supports the frequently rejected nest predation hypothesis (Lack 1968, Winkler and Walters 1983, but see Arnold et al. 1987), proposing that clutch size is limited by predation pressure due to increased incubation time for the longer laying period associated with more eggs in precocial birds. As precocial chicks evacuate the nest rapidly after hatching, limiting incubation time under high predation pressure may be a more effective response for precocial species, since only this phase is sensitive to whole brood loss (Perrins 1977). In contrast, it may be more advantageous for altricial species to increase the number of clutches, with fewer eggs in each, so that a high risk of whole-brood loss is spread among multiple breeding attempts (Martin 1995). Such an effect in altricial species would not be evident from our analysis of annual fecundity, in which we combined mean clutch sizes with annual number of clutches.

Nesting success

Life history pace was the only intrinsic factor that related to both fecundity and nesting success, however it only appeared as a significant predictor for success at the nestling stage, and only for cooperative breeders at the egg stage, but ultimately did not play a role in breeding success. Species with a slow pace of life have long developmental periods, which can expose offspring to a higher risk of predation and starvation. Furthermore, populations of cooperatively breeding species tend to have greater genetic similarity than other birds, which may result in reduced egg hatchability (Spottiswoode and Møller 2004). Such a deleterious effect of cooperative systems would be most detrimental to short-lived species, as any increase in reproductive failure could

have a substantial impact on fitness, while in long-lived species this effect may be mitigated by a large number of breeding attempts (Spottiswoode and Møller 2004).

Explanations for interspecific differences in breeding success, and how differences in breeding success relate to differences in fecundity, have so far received little attention. Remarkably, none of the intrinsic factors that influenced fecundity across species were related to breeding success (Fig. 6). Instead, breeding success depended on the species' breeding ecology. Unsurprisingly, low nest predation and high absolute latitude correlated with a high breeding success, and were important to success at both the egg and nestling stages. The seasonality of high latitudes is predicted to limit population density over harsh winters, which generates lower competition during the relatively high resource productivity of spring and summer (Ashmole 1963, Ricklefs 1980). Furthermore, the breadth of habitat usage appears critical in determining the relative reproductive success beyond hatching: specialists had greater breeding success than generalists, despite similar fecundity. This effect is puzzling, as populations of habitat specialists are declining at a faster rate than habitat generalists (Jiguet et al. 2007). While populations of habitat specialists appear more sensitive to changes in the environment (Keinath et al. 2017), our results suggest that their breeding success is higher compared to habitat generalists, requiring further investigation to understand the effect of habitat specialization on population vulnerability.

Nest predation rates can be temporally variable and sensitive to local changes at study sites, thus current estimates of nest predation may not reflect a species' evolutionary history of nest predation pressure (Martin 1995). A species' evolved nest type may be a better indicator of nest predation pressure in evolutionary time, but can also reflect other factors such as climate fluctuations, population density, or parasite abundance (Collias and Collias 2014). Yet, we found no link between nest type and annual fecundity or success, despite that it has been demonstrated to be a correlate of annual fecundity in a previous study (Martin 1995). This discrepancy may be due to the fact that we simplified the categorization of nest types into the basic categories "open" and "closed", while the previous study (Martin 1995) differentiated between closed nests that are excavated by the breeding birds or not. However, in our study, nest type was the major predictor of between-year variance in the annual number of eggs, nestlings, and fledglings, with open nests

having significantly higher variance of both fecundity and successful offspring. This suggests that population means of annual productivity are most sensitive to predation pressure in ecological time, while the evolutionary processes involved in determining a species' nest type are associated with variation in productivity. In particular, open nests are thought to provide flexibility to breeding birds, as open-nesting species have more choice in the location of their nest, which may be beneficial when dealing with variable environmental factors such as weather and predation pressure (Collias and Collias 2014). Consequently, open nesting species may be most sensitive to fluctuations in the environment, leading to greater phenotypic plasticity in reproduction.

Trade-offs between nest stages

Contrary to our expectations, success at either stage of nesting (and overall) was unrelated to annual fecundity, despite high variances of success across species. Therefore, species with a particularly small, or particularly large, annual number of eggs do not have greater reproductive performance relative to their investment. This result demonstrates that clutch size is not directly moderated by the probability of offspring survival to independence, nor vice versa, and suggests that females may not be able to regulate clutch size according to future breeding conditions (Erikstad et al. 1998). The inconsistency of results regarding nest success in clutch size manipulations within species (Dijkstra et al. 1990) further supports this view. Moreover, this result emphasizes that measures of fecundity relate differentially to breeding success among species and thus inferences of fitness based on numbers of eggs, especially in comparative studies, may be of limited usefulness and should be approached with care.

Conclusions

Across-taxa comparisons of life history strategies require that analogous measures are recorded among species. Yet, reproductive productivity is often measured at different stages of reproduction, which may differ in their selective pressures, among species. For species whose reproductive effort is completed at the time that the progeny separate from the parent (i.e. plants and animals with no post-oviposition parental care), reproductive effort directly corresponds to fecundity. However, in species with obligate parental care, reproductive effort does not terminate

until offspring attain independence from their parents. If the number of independent offspring varies independently of the number potential offspring (fecundity), and if constraints to success after oviposition or birth differ from those that affect fecundity, erroneous conclusions may be drawn for explanations of general patterns of life-history evolution.

Our comparative study indicates that inherent natural history traits best explain the evolved variation of fecundity in birds, but that the (often fluctuating) conditions of a species' breeding ecology is a better predictor of interspecific variation in nesting success in ecological time. Ideally, in birds, reproductive performance would be measured until the offspring attain independence rather than fledging, but we recognize that it is often problematic to follow the success of fledged offspring in natural populations and these data are less commonly investigated or reported. Nevertheless, natural selection acts on successful offspring, and may primarily shape reproductive investment, with fecundity functioning as only one of the mechanisms which optimizes that investment (Morris 1987). Thus, our findings emphasize that studies investigating measures of fitness and the evolution of reproductive strategies should focus on the selective pressures throughout an entire breeding cycle and reproductive performance be compounded once the full effort has been invested.

Acknowledgements

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2.6 Supplementary Material

Variable Definitions

Lifespan: Expected lifespan data for each species was either directly obtained from the literature or calculated from published adult survival data (references in Table S1), using the formula Lifespan= - (1/ln(survival rate)) (Seber 1982). For cases where life expectancy could not be obtained or calculated (N=4, all Psittaciformes), we recorded the longevity record for wild individuals. Although maximum recorded longevity can, in many cases, be much greater than life expectancy (Valcu et al. 2014), all species for which maximum longevity was used have few records of wild longevity and therefore are less likely to be skewed by exceptional individuals.

Developmental Mode: Species were categorized as precocial if they feed themselves upon hatching. All other species require provisioning and were categorized as altricial.

Nest Predation: The annual proportion of nests that were predated for each population were taken from the source paper whenever possible. When not provided, species-average nest predation rates were obtained from the major handbooks of birds (Cramp et al. 1994, Poole 2005, Higgins et al. 2007, Del Hoyo et al. 2011).

Nest Type: Nest types were categorized into a binomial variable of "closed" and "open" nests for simplicity. "Closed" nests is comprised of burrows, cavities, and closed cup nests. "Open" nests consists of both ground and arboreal open nests.

Diet: Species which only use one type of food listed below were categorised as food specialists while species that use at least two different food types were categorized as food generalists. Foods item categories used: plant materials (excluding flowers, nectar, pollen, fruit, seeds, nuts), seeds, nuts, insects and other invertebrates, animal flesh (vertebrates, including eggs, excluding fish), fish, flowers (including nectar and pollen).

Habitat: Categorized as 'specialist' or 'generalist'. The habitat in which species occur were categorized following the IUCN Habitats Classification Scheme. Species that occurred only in one habitat category were classified as specialists, while species that occurred in two or more habitat categories were classified as generalists.

Migration: Species were categorized as sedentary if they maximally showed local movements, while long-distance migrants were categorized as migratory.

Supplementary tables

Table S1: Species included in the analyses, with the years studied and latitude of each population. Sources include the original publications from which reproductive data was obtained as well as any additional sources of species characteristics included in analyses.

Species	Latitude	Years	Sources
Aimophila ruficeps	32.72	1997-1999	*(Morrison and Bolger 2002, Poole 2005)*
Aix sponsa	45.22	1986-1999	*(Mallory et al. 2002, Poole 2005)*
Amazona barbadensis	11	1990-1999	*(Sanz and Rodriguez-Ferraro 2006, Del Hoyo et al. 2011, Sekeris 2012)*
Amazona finschi	19.25	1996-2003	*(Renton et al. 2004, Salinas-Melgoza and Renton 2007, Del Hoyo et al. 2011)*
Amphispiza belli	42	1976-1980	*(Rotenberry and Wiens 1989, Poole 2005)*
Aphelocoma coerulescens	27.08	2000-2006	*(Poole 2005, Schoech et al. 2008)*
Ardea alba	37.56	1967-1979	*(Pratt and Winkler 1985, Poole 2005)*
Ardea herodias	40.12	1967-1979	*(Pratt and Winkler 1985, Poole 2005)*
Aythya valisineria	31.44	1980-2000	*(Kruse et al. 2003, Poole 2005)*
Bombycilla cedrorum	32.32	1964-1974	*(Leck 1979, Poole 2005)*
Bubulcus ibis	71.2	1974-1997	*(Telfair and Bister 2004, Poole 2005)*
Calcarius lapponicus	32.27	1967-1973	*(Custer and Pitelka 1977, Poole 2005)*
Campylorhynchus brunneicapillus	27.1	1973-1980	*(Marr and Raitt 1983, Poole 2005)*
Caracara cheriway	37.56	1994-1996	*(Morrison 1998, Poole 2005)*
Charadrius semipalmatus	58.45	1988-1995	*(Nol et al. 1997, Poole 2005)*
Chen canagica	63.39	1982-1986	*(Petersen 1992, Poole 2005)*
Cygnus columbianus	61.26	1988-2000	*(Babcock et al. 2002, Poole 2005)*
Dendrocopos minor	56.4	1989-1997	*(Cramp et al. 1994, Wiktander et al. 2001, Romero and Pérez 2008, Del Hoyo et al. 2011)*
Eclectus roratus	12.45	1997-2000	*(Higgins et al. 1990, Heinsohn and Legge 2003, Heinsohn et al. 2007, Del Hoyo et al. 2011)*
Eudyptula minor	-38.3	1986-2004	*(Higgins et al. 1990, Nisbet and Dann 2009)*
Falco berigora	-38	1999-2001	*(Higgins et al. 1990, Paul G. McDonald 2003, G MCDonald et al. 2004)*
Falco sparverius	42.39	1988-1992	*(Varland and Loughin 1993, Poole 2005)*
Ficedula hypoleuca	51.78	1948-1964	*(Harvey et al. 1985, Cramp et al. 1994, Del Hoyo et al. 2011)*
Ficedula hypoleuca	69.03	1975-1981	*(Järvinen and Väisänen 1984, Del Hoyo et al. 2011)*

Species	Latitude	Years	Sources
Gallinula chloropus	-31.5	1963-1985	*(NERCS , Harrison et al. 1997)*
Geospiza fortis	-0.42	1983-1998	*(Price and Grant 1983, Gibbs and Grant 1987, Gibbs 1988, Grant et al. 2000, Del Hoyo et al. 2011)*
Geospiza scandens	-0.67	1976-1998	*(Price and Grant 1983, Grant 1984, Gibbs and Grant 1987, Grant et al. 2000, Del Hoyo et al. 2011)*
Lagopus lagopus scoticus	56.9	1957-1961	*(Jenkins et al. 1963, Del Hoyo et al. 2011)*
Lanius ludovicianus	40.65	1969-1972	*(Porter et al. 1975, Brooks and Temple 1990, Poole 2005)*
Lanius minor	40.35	1989-1997	*(Kristin et al. 2000, Krištín et al. 2007, Del Hoyo et al. 2011)*
Lophodytes cucullatus	45.22	1986-1999	*(Mallory et al. 2002, Poole 2005)*
Malurus pulcherrimus	-31.11	1993-1998	*(Higgins et al. 1990, Brooker and Brooker 2001, Rowley and Russell 2002)*
Malurus splendens	-31.95	1973-1989	*(Higgins et al. 1990, Rowley et al. 1991, Russell and Rowley 1993)*
Meleagris gallopavo	40.19	1981-1985	*(Vangilder et al. 1987, Poole 2005)*
Melospiza melodia	48.65	1977-1984	*(Hochachka 1990, Arcese et al. 1992, Poole 2005)*
Merops bullockoides	-0.37	1977-1983	*(Emlen and Wrege 1991, Wrege and Emlen 1991, Del Hoyo et al. 2011)*
Mycteria Americana	28.1	1981-1985	*(Rodgers and Schwikert 1997, Poole 2005)*
Oreoscoptes montanus	42	1976-1980	*(Rotenberry and Wiens 1989, Poole 2005)*
Parabuteo unicinctus	32.76	1981-1983	*(Bednarz 1987, Poole 2005)*
Parus major	55.41	1983-1987	*(Smith et al. 1989, Del Hoyo et al. 2011)*
Perisoreus infaustus	65.4	1992-2012	*(Ekman and Griesser 2016)*
Petrochelidon pyrrhonota	30.2	1982-1985	*(Kosciuch et al. 2001, Poole 2005)*
Picoides borealis	35.17	1980-1985	*(LaBranche and Walters 1994, Poole 2005)*
Platalea minor	41.8	1999-2003	*(Guo-An et al. 2005, Del Hoyo et al. 2011)*
Plectrophenax nivalis	74.52	1966-1969	*(Hussell 1972, Poole 2005)*
Prionops plumatus	-31.5	1971-1974	*(NERCS , Harrison et al. 1997)*
Procellaria westlandica	-42.14	1995-2003	*(Higgins et al. 1990, Waugh et al. 2006)*
Progne subis	42.28	1938-1940	*(Allen and Nice 1952, Poole 2005)*
Pygoscelis adeliae	-74.21	1995-2005	*(Higgins et al. 1990, Pezzo et al. 2007, Del Hoyo et al. 2011)*
Pyrrhula pyrrhula	52.03	1974-1979	*(Bijlsma 1980, Cramp et al. 1994, Del Hoyo et al. 2011)*
Rhynchopsitta pachyrhyncha	28.3	1995-2001	*(Monterrubio et al. 2002, Poole 2005)*
Rissa tridactyla	64.34	1975-1989	*(Murphy et al. 1991, Poole 2005)*
Saxicola dacotiae	28.46	2000-2002	*(Illera and Diaz 2006, Del Hoyo et al. 2011)*
Sialia mexicana	39.1	2005-2010	*(NestWatch , Poole 2005)*
Sialia mexicana	45.5	1997-2001	*(Keyser et al. 2004, Poole 2005)*
Sialia sialis	35.5	1999-2004	*(Poole 2005, Stanback and Seifert 2005)*

Species	Latitude	Years	Sources
Sitta carolinensis	39	2005-2010	*(NestWatch , Poole 2005)*
Sitta europaea	60	1986-1990	*(Pravosudov 1993, Del Hoyo et al. 2011)*
Somateria mollissima	55.35	1958-1998	*(Coulson 1999, Poole 2005)*
Spizella breweri	42	1976-1980	*(Rotenberry and Wiens 1989, Poole 2005)*
Stercorarius parasiticus	60.08	1979-1994	*(Phillips et al. 1996, Poole 2005)*
Sterna dougallii	-4.2	1995-2001	*(Ramos et al. 2002, Poole 2005)*
Tachycineta bicolor	38.98	2006-2010	*(NestWatch , Poole 2005)*
Thinornus rubricollis	-38.28	1992-1995	*(Higgins et al. 1990, Baird and Dann 2004)*
Vanellus coronatus	-31.5	1965-1993	*(NERCS , Harrison et al. 1997, Del Hoyo et al. 2011)*
Xema sabini	75.49	2007-2011	*(Poole 2005, Mallory et al. 2012)*
Xema sabini	64.55	1980-2001	*(Poole 2005, Mallory et al. 2012)*
Zonotrichia leucophrys	37.77	1975-1980	*(Petrinovich and Patterson 1983, Poole 2005)*

Table S2: Standardized principal components loadings and communality (h^2) of continuous factors. Eigenvalues and cumulative variance explained by each component are also given.

	loadings		h^2
	PC1: life history pace	PC2: nest predation	
body mass	**0.79**	0.20	0.66
adult survival	**0.80**	-0.01	0.64
nest predation	-0.15	**0.98**	0.98
eigenvalue	1.28	1.00	
cumulative variance explained (%)	0.43	0.76	

Table S3: Estimates, credible intervals and p-values of reduced model testing mass-specific annual fecundity (Sibly et al. 2012). Estimates are reported as differences between respective fixed-term categories and the intercept (alphabetically first category in a given fixed effect). "DM" indicates developmental mode.

	Estimate	95% Credible Interval		pMCMC
		Lower	Upper	
Intercept	0.01	-0.53	0.39	0.85
Life history pace	-0.61	-0.77	-0.43	<0.001
Nest predation	0.11	-0.07	0.28	0.21
DM: precocial	0.87	0.23	1.56	0.010
Migration	-0.41	-0.75	-0.09	0.014
Nest predation x DM: precocial	-0.89	-1.46	-0.33	0.002

Table S4: Estimates, credible intervals and p-values of reduced model testing the between-year variance of annual fecundity. Estimates are reported as differences between respective fixed-term categories and the intercept (alphabetically first category in a given fixed effect).

	Estimate	95% Credible Interval		pMCMC
		Lower	Upper	
Intercept	0.22	-0.40	0.88	0.46
Mean annual fecundity	0.61	0.41	0.83	<0.001
Absolute latitude	-0.014	-0.024	-0.003	0.018
Nest type: open	0.53	0.17	0.90	0.010

Table S5: Estimates, credible intervals and p-values of reduced model testing the between-year variance of annual number of hatchlings. Estimates are reported as differences between respective fixed-term categories and the intercept (alphabetically first category in a given fixed effect).

	Estimate	95% Credible Interval		pMCMC
		Lower	Upper	
Intercept	-0.40	-0.91	0.16	0.14
Mean annual hatchlings	0.56	0.34	0.78	<0.001
Nest type: open	0.79	0.39	1.28	<0.001

Table S6: Estimates, credible intervals and p-values of reduced model testing the between-year variance of annual number of fledglings. Estimates are reported as differences between respective fixed-term categories and the intercept (alphabetically first category in a given fixed effect).

	Estimate	95% Credible Interval		pMCMC
		Lower	Upper	
Intercept	-0.49	-0.97	0.02	0.07
Mean annual fledglings	0.62	0.35	0.90	<0.001
Nest type: open	1.00	0.41	1.47	<0.001

Chapter 3

Perceived nest predation risk prior to breeding influences reproductive allocation strategy and nesting success in birds

Gretchen F. Wagner [1], Emeline Mourocq[1], Michael Griesser[1]

[1] Department of Anthropology, University of Zürich, Zürich, Switzerland

Chapter 3

3.1 Abstract

Offspring predation is the primary source of reproductive failure in many species and the mere fear of offspring predation can shape the evolution of reproductive decisions. Yet, it remains unclear why phenotypic responses to an increased risk of offspring predation vary across species, and if temporary changes in risk prior to a reproductive attempt have downstream effects on breeding success. Here we temporarily increased the perceived risk of nest predation prior to egg-laying in eight bird species to assess interspecific variation in risk-dependent changes to reproductive allocation and success. Contrary to prevailing theory, there was no clear pattern of a reduction to clutch size across species, however clutch volume and nesting success were generally reduced under an increased perceived risk. Furthermore, species with a prolonged parent-offspring association increased their within-clutch variation in egg volume. This novel finding suggests that birds may diversify their reproductive allocation under a high perceived nest predation risk, and highlights that the duration of parent-offspring association can affect early allocation decisions. We demonstrate that a temporary change in predation risk at a critical moment of reproductive decision-making can have delayed consequences on fitness, emphasizing that rapid temporal variation in predation risk may favor the evolution of reproductive flexibility in birds.

3.2 Introduction

Predation of eggs or dependent young is a major cause of reproductive failure, affecting the evolution of reproductive allocation (Ricklefs 1969, Martin 1995, Martin and Briskie 2009). The mere fear of predation can influence the behavior, condition, fitness, and population dynamics of prey, sometimes even surpassing the lethal effects of direct predation (Lima 1998, Preisser et al. 2005, Cresswell 2008). Therefore, fear of offspring predation may critically shape reproductive decisions to decrease the probability of offspring mortality (Creel and Christianson 2008, Martin and Briskie 2009). However, the benefits derived from fear can be offset by costs, such as reduced reproductive success, even in the absence of direct predation (Preisser et al. 2005, Zanette et al. 2011).

Natural predation risk is ubiquitously variable and can change rapidly over time and space. Consequently, field studies have investigated changes in parental decisions over natural risk gradients (Zanette et al. 2006, Thomson et al. 2011) and in response to experimental modifications of perceived risk (Fuller and Berglund 1996, Ghalambor et al. 2013). In birds, field experiments have demonstrated that parents can alter their reproductive investment depending on the perceived nest predation risk (Eggers et al. 2006, Zanette et al. 2011, Hua et al. 2014). However, these single-species investigations have yielded contrasting results, suggesting that species differ in their responses (Ibáñez-Álamo et al. 2015), which was confirmed by a recent comparative study (LaManna and Martin 2016). These studies increased the perceived risk of nest predation from before egg-laying until after offspring fledging (Zanette et al. 2011, Hua et al. 2014, LaManna and Martin 2016; but see Eggers et al. 2006), providing insights into the influence of generally high or low predation risk on reproductive investment and success. However, anti-predator responses can depend on the frequency and duration of high-risk situations (Lima and Bednekoff 1999, Ferrari et al. 2009), and it remains unknown if temporary increases in risk levels early in a reproductive cycle have downstream effects on reproductive decisions and reproductive success. The initial reproductive allocation sets the upper limit for the number of offspring produced, and must be weighed against the effort it will require to raise the offspring and the probability of their survival.

A temporary increase in the perceived risk to forthcoming offspring prior to egg-laying may therefore have detrimental effects on the success of that reproductive event.

Here we investigated differences in the reproductive responses of eight bird species to an experimentally increased perceived risk of nest predation prior to egg laying. We examined how life-history and ecological factors influence the risk sensitivity of an individual in ecological time. Comparative experimental studies such as this one face an important challenge: it is preferable that all study species are confronted with identical stimuli. However, this approach does not always result in a comparable stimulus among species. For example, a common jay (Garrulus glandarius) is a common nest predator of open nests but does not pose a risk to the nests of cavity-breeding species. Thus, to compare the response of species which vary in their life history and ecology, we used the predator(s) which represent a high risk for each species. In most cases these predators were avian, and we used vocalizations to simulate their presence. However, in two of our study species (*Oenanthe leucura, Merops apiaster*) we rarely or never observed nest predation by avian predators, and so we presented live, confined rats (*Rattus norvegicus*) as the stimulus. This design generates important caveats: different predator types (e.g., mammalian vs. avian) may in themselves present different risks due to diverse hunting techniques and behavior, and the structure of the stimulus (auditory only vs. auditory + visual) may elicit different responses. Therefore, to ensure that differences in responses were not based on the stimulus type *per se,* we include the stimulus type as a factor in all analyses. Furthermore, in many small bird species, rats present a risk to adults as well as offspring, however in the species studied here we have never observed a rat predating an adult on the nest (throughout several years of video recording), and we know of no cases reported in the literature (Soler et al. 1995, Petrescu and Costica 2001).

Following life-history theory, we expect that species with a slow life history pace are the most sensitive to adverse breeding conditions (Roff 1993, Erikstad et al. 1998), and consequently reduce their allocation in a risky environment. The plasticity of responses to nest predation risk should also vary depending on the level of risk (Ghalambor et al. 2013, LaManna and Martin 2016), thus species with naturally high nest predation rates and more vulnerable nest structures are expected to be most sensitive to an experimental increase in the perceived risk of predation. Furthermore,

species with extended post-fledging parent-offspring association (i.e., family-living, Drobniak et al. 2015) are predicted to lay smaller eggs when faced with high nest predation risk, as these species have a greater opportunity to compensate for poor offspring condition than species with prompt offspring dispersal.

A widespread response to variable and/or unpredictable environments is an increased variance in investment across offspring (Crump 1981, Koops et al. 2003, Marshall et al. 2008). In birds, within-clutch differences in egg size can result in a hierarchy among nestlings (Slagsvold et al. 1984, Arnold 1991), allowing parents to selectively raise the strongest offspring if poor conditions persist, but maintain the possibility of raising all offspring if conditions improve (Lack 1947). Birds often reduce the provisioning rate to nests in the presence of nest predators (Eggers et al. 2005b, Ghalambor et al. 2013, Schneider and Griesser 2015), and birds breeding in unpredictable environments particularly neglect offspring in poor condition (Caro et al. 2016). Based on these ideas we speculated that female birds may also increase the variance in egg size in response to variable nest predation risk (Hussell 1972), but this hypothesis has not been previously tested.

3.3 Material and Methods

Study species and sites

Data for this study were collected from seven bird species in Southern Spain in 2011-2014 and one species in Northern Sweden in 2004 (Table 1). In Spain, the experiment was conducted in populations of great tits (*Parus major*) and spotless starlings (*Sturnus unicolor*) near Cordoba (37°95'N, 4°40'W), black wheatears (*Oenanthe leucura*), European bee-eaters (*Merops apiaster*), red-billed choughs (*Pyrrhocorax pyrrhocorax*) and long-tailed tits (*Aegithalos caudatus*) near Guadix (37°25'N, 3°05'W), and common blackbirds (*Turdus merula*) near Lecrín (36° 56'N, 3° 33'W). Siberian jays (*Perisoreus infaustus*) were studied near Arvidsjaur in Northern Sweden (65°40'N, 19°7'E). For this species, we used previously published data (Eggers et al. 2006), including only the data from the year that the experimental design corresponded with the one used in Spain. To ensure that fundamental differences between the species studied in Spain and

Sweden do not drive our findings, we re-ran our analyses excluding the Siberian jay, which yielded analogous results (Tables S3-S6).

Table 1. Study species differ in life history and ecology. 'N pred.' is the number of nests in the predator treatment group and 'N cont.' is the number of nests in the control group. 'Time in nest' is the average number of days from egg laying until fledging, 'post-fledging time' is the average number of days spent in association with parents after fledging.

species		experiment			species traits							
common name	scientific name	N pred	N cont	year	body mass (g)	adult survival (%)	nest type	no. of broods	mean clutch size	nest time (d)	post-fledging time (d)	nest predation (%)
Black wheatear	*Oenanthe leucura*	8	9	2012	36	49.5	closed	2.5	4.0	31	200	28.6
Common blackbird	*Turdus merula*	8	19	2011	94	56.0	open	2.5	2.9	27	21	21.7
European bee-eater	*Merops apiaster*	11	12	2013-2014	52	49.8	closed	1.0	5.7	57	250	22.8
Great tit	*Parus major*	10	10	2012	17	48.6	closed	1.5	7.5	37	30	36.9
Long-tailed tit	*Aegithalos caudatus*	9	11	2013	7	55.0	open	1.0	7.3	32	300	77.8
Red-billed chough	*Pyrrhocorax pyrrhocorax*	13	16	2013-2014	310	80.0	closed	1.0	4.7	56	42	7.7
Siberian jay	*Perisoreus infaustus*	9	9	2004	84	69.0	open	1.0	3.9	42	400	15.6
Spotless starling	*Sturnus unicolor*	13	8	2012	74	49.9	closed	2.0	4.6	34	7	26.3

Experimental design

We manipulated the perceived risk of nest predation by simulating an increased presence of nest predators in nesting areas prior to egg laying. We selected common nest predators for each species based on multiple years of nest monitoring. For each species, nesting areas were randomly assigned to either a predator treatment group or a control group while balancing the sample sizes. For the predator treatment of open-nesting species (Table 1) we play-backed calls of locally occurring corvids (*Pica pica*, *Garrulus glandarius, Corvus corone, Corvus corrax)*, for closed-nesting species whose principal nest predators are avian, we played calls of woodpeckers (*Dendrocopos major, Picus viridis)*, and for two closed nesting species (black wheatear, European bee-eater) whose nest predators were mainly small mammals or snakes, we presented a live brown rat

(*Rattus norvegicus*) in a transparent plastic box. The control treatment consisted of a playback of locally occurring non-threatening species' calls (pigeons: *Columba palumbus* and *Streptopelia turtur,* or songbirds: *Turdus merula* and *Carduelis chloris*) or presence of a harmless mammal (European rabbit, *Oryctolagus cuniculus*).

Playbacks in Spain were presented daily from 07:00-19:00, with 12 hours of silence played overnight. Each 12-hour period of calls was comprised of a unique combination of 15-30 seconds of calls, separated by 4 minutes of silence. Calls were downloaded from www.xeno-canto.org. Each playback unit was comprised of a box with battery, amplifier, speaker, and mp3 player, and was placed on the ground, covered with a camouflage cloth. Live animals were kept in the territories continuously. All nests were visited every 1-3 days to maintain the treatments (change batteries, care for animals) and to check nest contents. The locations of playbacks and mammals were changed during each visit. The details of the playbacks used for Siberian jays can be found in Eggers et al. (2006); the only difference in the set-up was that territories were only exposed every second day to playbacks due to field logistics.

Nest areas were determined through three methods. The experimental location was based on previous nests for species with consistent nest locations across years (black wheatear, red-billed chough, Siberian jay) or nests were located early in the construction phase (long-tailed tit, European bee-eater, great tit). For two densely nesting species (common blackbird, spotless starling), we placed playbacks throughout the study area and subsequently located nests that were within the area the playbacks were audible (mean nests per playback: common blackbird=2.08, spotless starling=1.75). Across all species, playbacks were located a mean distance (±SE) of 43±2.5m from the nests. Mammals were located 26±1.5m from the nests. We began the experiment approximately 10 days prior to egg laying in all species, which was estimated based on the phenology of previous breeding seasons and/or nest-building progress. On average, nests were exposed for 9.6±0.14 days. The treatments were removed within three days of the onset of egg laying (mean time between start of exposure and onset of egg laying=8.2 days).

Once a clutch was complete, we measured the length and width of all eggs using dial calipers (0.1mm accuracy). Individual egg volume was calculated using the formula

volume=0.51(length)*(breadth)*^{2} (Hoyt 1979). Nests were monitored throughout the breeding cycle. The number of eggs, hatchlings and fledglings, and any nest failures, were recorded for each nest. The number of fledglings was assessed based on the number of nestlings in the nest prior to fledging (<3 days) and/or observations of juveniles after fledging. Nest failures were assumed to be caused by predators if: (i) predation was documented through direct observation or recording, (ii) the entire clutch or brood disappeared prematurely, or (iii) evidence, such as punctured eggs, or albumen or blood on nest material, was discovered. We were unable to identify the source of other nest failures, but causes may include nest abandonment, parental death, parasitism, starvation or adverse weather.

Statistical Analyses

All statistical tests were conducted with R 3.1.0 (R Core Team 2014). Because many life-history traits within a species are correlated (Stearns 1992), we ran a principal components analysis (PCA; package 'psych', Revelle 2015) on continuous species traits of interest (adult survival probability, body mass, nesting time, and post-fledging parent-offspring association time; see Table 1) to identify significant combinations of these traits and to create new uncorrelated variables. We relied on the correlation matrix among variables (Table S1) to generate PCA scores rather than the covariance matrix (Graham 2003) because the units of measurement for traits differed. The inspection of a scree plot and eigenvalues (package 'nFactors', Raiche 2010) suggested the extraction of 2 components. We first performed an oblique (oblimin) rotation of the components to simplify the factor structure by maximizing the variances of loadings, which indicated that the resulting factors were not correlated (r=-0.11). We then applied a varimax rotation to the original components. Differences in results of the rotation techniques were negligible, and did not influence the pattern of loadings, so we retained the oblimin rotation in further analyses (Kieffer 1998). The two components extracted from the PCA cumulatively accounted for 89% (60 and 29%, respectively) of the total variance in the included species traits. The first component, labelled “life-history pace”, included adult body mass, nesting time (from egg-laying until fledging), and adult survival (Table S1). High values of this component represent large-bodied, long-lived, slow-

developing species. The second component, labelled “time post-fledging”, included only the post-fledging association time of offspring with their parents (Table S1).

To examine among-species patterns of experimental effects on clutch size, egg volume, clutch volume, within-clutch variation of egg volume, number of hatchlings and number of fledglings we ran separate (generalized) linear mixed models (GLMM; package 'nlme', Pinheiro et al. 2014). All models initially included the experimental treatment (predator, control), nest type (open, closed), natural predation risk (percent of non-experimental nests lost to predation in the year of the experiment), number of broods (species-average number of successful broods per year), and the two PCs (life-history pace, time post-fledging) as explanatory variables. Relative laying date (the number of days since the first egg of the year for each species), stimulus type (mammalian, avian), and mean distance between each nest and the experimental stimuli were included as potential covariates. The interactions between the experimental treatment and each of those factors were also included in initial models. Clutch size was included as a covariate for all models except that of clutch size itself. Year and species identity were included as random factors in all models, and nest identity was additionally included as a random factor in the model of egg volume.

Only completed clutches were included in these analyses. We were unable to obtain egg measurements in some nests due to nest inaccessibility or early egg breakage (n=19 across species) and those nests were excluded from analyses of egg or clutch volume (see Table S3 for sample sizes). Clutch volume was log-transformed prior to analyses. Continuous variables were scaled to unit variance and centered to facilitate the comparison of effects of multiple explanatory variables (Schielzeth 2010). Models of clutch size, number of hatchlings and number of fledglings were fitted with a Poisson distribution, all other response variables assumed a reasonably Gaussian distribution. Appropriate model fits were confirmed with chi-square tests of the residual deviance and inspection of the residual distributions.

We examined whether nests were more likely to fail or succeed according to the experimentally increased risk of nest predation prior to egg laying. We fit binary (logit link) Markov chain GLMMs (package 'MCMCglmm', Hadfield 2010) for overall nest success, and nest success at each stage of nesting (fail/succeed at egg stage, fail/succeed at nestling stage for nests that hatched at least one

egg). The same parameters were used as listed above for the models of reproductive traits. The models were run for 100'000 iterations, with a burn-in period of 2'000 iterations and a thinning interval of 100, which resulted in approximately 1'000 samples from the posterior distributions for each model parameter. We specified an inverse gamma prior, with the random effects variance set as V=1 and nu = 0.002. Residual error was fixed at one. Model convergence was confirmed by visual examination of trace plots and calculation of autocorrelation between iterations.

Non-significant ($p>0.10$) interactions between main effects and main effects were sequentially removed from models to attain a minimal adequate model (Crawley 2002), except the experimental treatment, which was retained in all models. Estimates of non-significant terms were acquired from fitting each non-significant term individually into the minimal model (Crawley 2002). Values for non-significant interactions are not reported.

3.4 Results

Analyses were based on 175 nests of eight species (Table 1). Assessment of clutch volume indicated that females in the predator treatment had reduced clutch volume across species, while controlling for significant effects of natural differences related to actual predation risk, relative laying dates, and clutch sizes (Table 2). An increased within-clutch variation in egg volume was associated with prolonged associations between offspring and parents in the nest predator treatment group (Fig. 1), while controlling for a significant effect of the treatment's proximity to the nest (Table 2).

Clutch size was not influenced by the experimental treatment when controlling for significant influences of natural predation risk, number of broods, and nest type (Table 3), nor did any included factor explain interspecific differences in treatment effects. No included factor explained interspecific differences in the treatment effects on egg volume (Table 2).

Table 2. Model estimates and corresponding standard errors and p-values for predictors of allocation into eggs. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est.=estimate, p=p-value.

	egg volume			clutch volume			egg volume variation		
fixed effects	est.	SE	p	est.	SE	p	est.	SE	p
intercept[1]	0.04	0.11	0.73	0.09	0.29	0.75	-0.11	0.18	0.55
treatment (predator)[2]	0.001	0.02	0.97	**-0.05**	**0.02**	**0.04**	0.20	0.14	0.15
life-history pace	**0.97**	**0.13**	**<0.01**	**1.10**	**0.36**	**0.03**	-0.14	0.18	0.44
time post-fledging	0.06	0.18	0.74	0.46	0.44	0.35	-0.03	0.17	0.88
number of clutches	**0.24**	**0.11**	**0.07**	0.50	0.33	0.19	-0.39	0.27	0.21
predation risk	0.07	0.05	0.21	-0.50	0.20	0.24	0.14	0.15	0.36
nest type (open)[2]	0.11	0.25	0.68	-0.09	0.69	0.90	-0.41	0.35	0.31
laying date	**-0.02**	**0.01**	**0.08**	**-0.07**	**0.02**	**<0.01**	-0.06	0.12	0.62
predator type (mammalian)[2]	-0.07	0.27	0.80	0.41	0.72	0.59	-0.12	0.64	0.86
proximity to nest	0.02	0.03	0.44	0.02	0.03	0.60	**-0.49**	**0.17**	**<0.01**
clutch size	0.02	0.02	0.24	**0.34**	**0.02**	**<0.01**	0.10	0.07	0.13
treatment (predator)[2] x number of clutches				**-0.06**	**0.03**	**0.03**			
treatment (predator)[2] x time post-fledging							**0.41**	**0.16**	**<0.01**
random effects									
species	1.59			0.80			0.36		
year	<0.01			<0.01			<0.01		
nest	0.52								

[1] Reported intercepts are from reduced models, which include only the fixed effects in bold.

[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table 3. Model estimates and corresponding standard errors and p-values for predictors of the number of offspring at each nest stage. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est. =estimate, p=p-value.

	clutch size			number of nestlings			number of fledglings		
fixed effects	**est.**	**SE**	**p**	**est.**	**SE**	**p**	**est.**	**SE**	**p**
intercept[1]	**1.70**	**0.05**	**<0.01**	**0.41**	**0.15**	**<0.01**	**0.93**	**0.30**	**<0.01**
treatment (predator)[2]	-0.04	0.07	0.55	0.05	0.08	0.55	0.08	0.11	0.44
life-history pace	**-0.12**	**0.05**	**0.02**	0.04	0.04	0.31	0.06	0.05	0.23
time post-fledging	-0.01	0.05	0.79	0.03	0.04	0.53	-0.01	0.06	0.82
number of clutches	**-0.17**	**0.04**	**<0.01**	-0.10	0.08	0.24	-0.16	0.09	0.09
predation risk	**0.23**	**0.04**	**<0.01**	0.000	0.002	0.97	0.002	0.004	0.59
nest type (open)[2]	**-0.39**	**0.09**	**<0.01**	0.02	0.09	0.82	-0.14	0.12	0.25
laying date	0.002	0.04	0.96	-0.002	0.004	0.59	0.001	0.004	0.87
predator type (mammalian)[2]	-0.05	0.09	0.59	0.02	0.10	0.86	0.09	0.13	0.49
proximity to nest	0.02	0.05	0.70	-0.02	0.05	0.64	-0.04	0.06	0.48
clutch size	n.a	n.a.	n.a.	**0.20**	**0.03**	**<0.01**	**0.13**	**0.04**	**<0.01**
random effects									
species	0.02			<0.01			<0.01		
year	<0.01			<0.01			<0.01		

[1] Reported intercepts are from the reduced models, which include only the fixed effects in bold.

[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

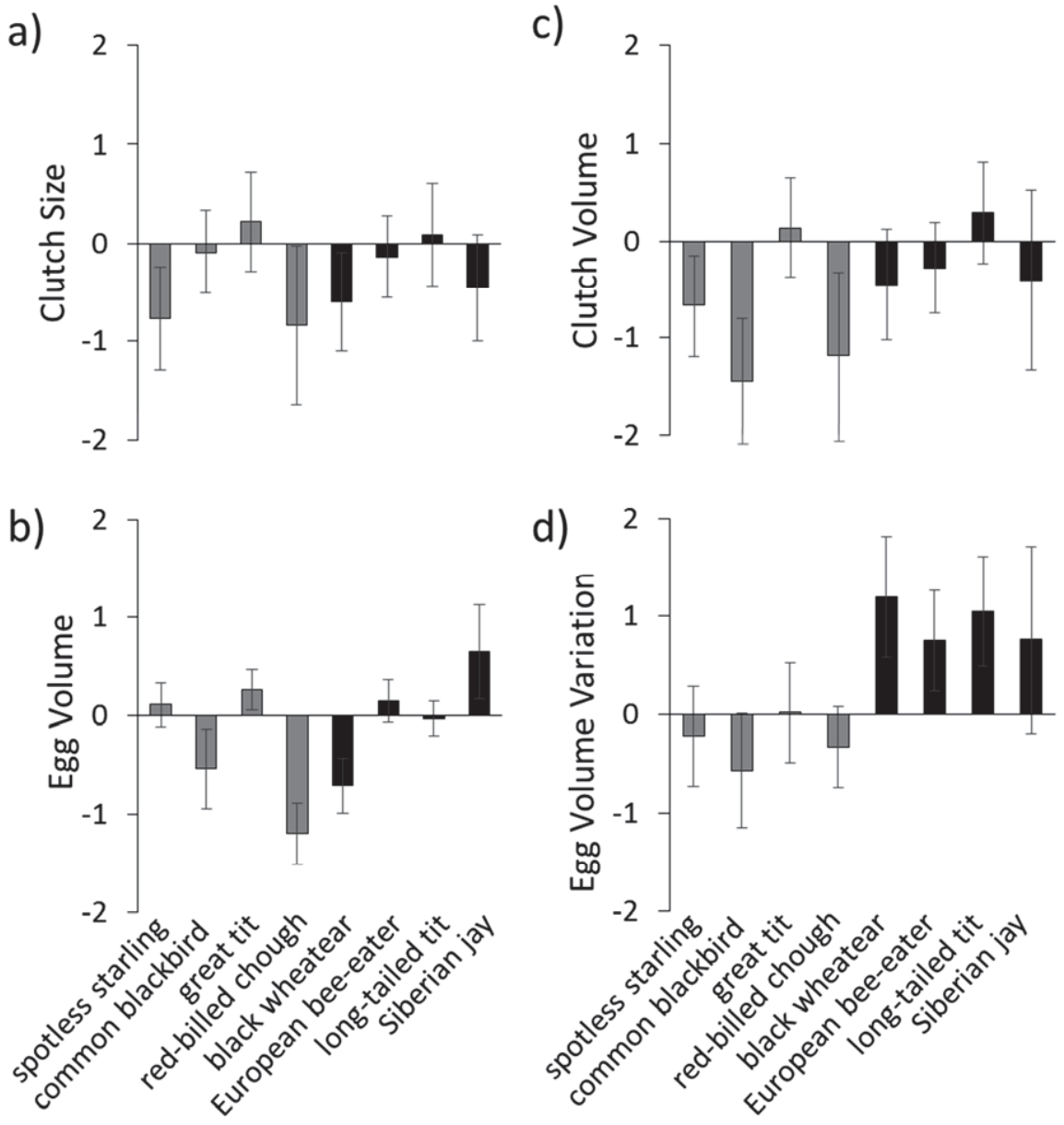

Fig. 1. Reproductive allocation responses to an experimental increase in perceived risk of nest predation prior to egg-laying. Responses are standardized effect sizes (Cohen's d ± 1 SE, Table S2). Negative values reflect a decrease in the treatment group compared to the control group. Species are arranged in order of increasing post-fledging time with parents; grey bars represent non-family-living species, black bars represent family-living species (according to Drobniak et al. 2015). When faced with an increased perceived risk, females either did not adjust, or marginally reduced, (a) clutch size and (b) egg volume. These factors combined to generate a more general decrease in (c) clutch volume. (d) An increased within-clutch variation of egg volume (coefficient of variation) was found in family-living species.

Experimental nests tended to be more likely to fail to fledge any offspring than control nests (odds ratio= 2.20, 95% credible interval= 1.07 to 5.37, p=0.06, Fig. 2) when controlling for natural nest predation rates (Table S3). This effect was particularly pronounced during the nestling stage (odds ratio= 3.74, 95% credible interval= 1.15 to 12.43, p= 0.01, Table S3). At the egg stage, only open nesting species in the predator treatment were more likely to experience nest failure (treatment x nest type: odds ratio= 8.94, 95% credible interval= 1.19 to 64.07, p= 0.02), while controlling for natural differences in failure rates between the predator type and post-fledging time with parents (Table S3). These results are unlikely to reflect differences in direct nest predation: the proportion of predated nests did not differ between the experimental and control groups (29.6% vs. 23.7% respectively, N=46 nests, p=0.37). In successful nests, the number of hatchlings (mean weighted effect size=0.01±0.25, p=0.97) and the number of fledglings (mean weighted effect size=0.10±0.27, p=0.71) did not differ between the treatment groups among species (Table S2), nor did any included factor explain interspecific differences in these responses to the treatment (Table 3).

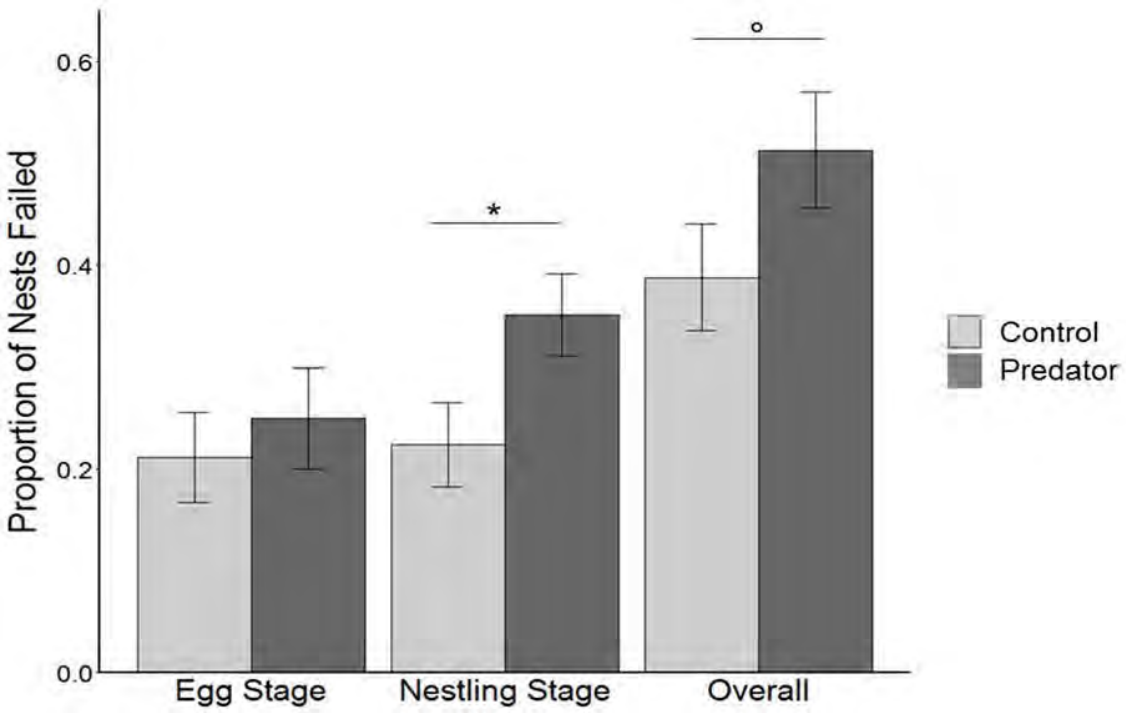

Fig. 2. Nests exposed to an increased perceived risk of predation were more likely to fail. Treatment and control means (± 1 SE) at the egg stage, nestling stage, and overall. *p<0.05; °p<0.10.

3.5 Discussion

Nest predation is the primary source of reproductive failure in many avian populations and is likely to impose selection for adaptations that reduce nest predation risk and/or the costs associated with nest predation. Our comparative experiment corroborates that species vary in their responses to an increased perceived risk of nest predation (Ghalambor et al. 2013, LaManna and Martin 2016), and demonstrates that a temporarily increased nest predation risk prior to egg-laying can have detrimental downstream effects on reproductive success. In general, birds showed a decrease in clutch volume when faced with an increased risk, a combined effect of minor reductions to clutch size and egg volume. In addition, we show for the first time that birds may respond to a high risk of nest predation by altering the distribution of their reproductive allocation across their eggs, resulting in a marked increase in within-clutch variation of egg volume. This response predictably varied with prolonged parent-offspring association. These findings lend further support to the importance of nest predation in shaping reproductive investment decisions and success in birds (Lima 2009, Ibáñez-Álamo et al. 2015), and highlight that species differ in the strength and nature of their response depending on their post-fledging association with their offspring.

Predation risk can fluctuate considerably over time, and the perceived risk of nest predation early in a reproductive cycle may not reflect the actual risk of nest predation later on. Brood reduction, which is facilitated by variation in egg size (Slagsvold et al. 1984), may be an adaptive strategy to cope with unpredictable environments (Caro et al. 2016). If high predation risk prevails throughout the nesting period, a smaller number of nestlings may reduce the risk of whole brood failure through reduced nest attentiveness (Eggers et al. 2008, Ghalambor et al. 2013). However, if all offspring survive, parents may compensate for offspring condition asynchronies through prolonged post fledging care and/or preferential care of lesser offspring once the high risk period has passed (Shizuka and Lyon 2013). Our results give support to a compensation strategy, as a risk-dependent increase in within-clutch variation in egg volume was only found in species with a long post-fledging parent-offspring association. In these species, parents have a greater opportunity to balance out offspring quality after their offspring have fledged, which may allow for greater

flexibility in reproductive allocation. Indeed, species with prolonged parent-offspring association not only have longer durations of post-fledging parental care, but this period can be highly variable and have significant consequences for offspring survival (Green and Cockburn 2001, Griesser et al. 2006).

Theory predicts that breeding birds should decrease their reproductive investment when faced with a high risk of nest predation (Roff 1993). While decreases in clutch size have been found in some experimental studies of individual species (Eggers et al. 2006, Zanette et al. 2011, Hua et al. 2014), neither our investigation nor previous comparative work (Yanes and Suárez 1997, Fontaine and Martin 2006, LaManna and Martin 2016) have found a strong general pattern of clutch size varying with predation risk. Because any change in clutch size is necessarily incremental, this response cannot allow for a fine adjustment of investment. Therefore, continuous changes to egg size may be a more prudent response, considering the unpredictable nature of predation risk (Fontaine and Martin 2006). Adjustments to egg mass were found in a previous comparative study, however the direction of the responses differed depending on the species' re-nesting potential: species with multiple broods reduced egg mass, while single-brood species increased egg mass (LaManna and Martin 2016). Among the species studied here, we found no general pattern of changes to egg volume, nor were treatment differences in egg volume related to the number of broods or any other investigated factor. More work is required to determine if these patterns differ due to differences in reaction norms, the responses measured, or study design. Nevertheless, we found a general trend of a reduction to clutch volume among the tested species, resulting from joint effects of minor adjustments to egg and clutch sizes. Adjustments to clutch size and egg size are probably variants of the same response (Zanette et al. 2011), and thus the overall effects are most clear when measured as the total combined investment into offspring quantity and quality (i.e., clutch volume).

Nests exposed to an experimental increase in the perceived risk of nest predation prior to egg-laying were less likely to fledge offspring than control nests, particularly due to failure during the nestling stage. There was no difference in the number of fledglings from successful nests, indicating that whole-brood loss was the driving factor for experimental differences in

reproductive success. Yet, the proportion of nest failures caused by direct nest predation did not differ between the experimental and control nests, suggesting that other causes of failure were responsible for this difference (e.g., abandonment or starvation). Previous studies have reported decreased reproductive success when the perceived risk of nest predation was high throughout the entire breeding cycle (Zanette et al. 2011, Hua et al. 2014, LaManna and Martin 2016). Consequently, differences in reproductive success have been attributed to combined effects of parental decisions under high risk during egg-laying, incubation and provisioning. Our experimental treatment was removed at the onset of egg-laying, highlighting that the conditions, and resultant investment decisions, at the laying stage can impact reproductive success even if conditions improve. Because risk can be transitory and decisions made under high risk can be costly, it would be adaptive to make substantial adjustments to behavior only under an immediate threat. Thus, we suggest that the here observed decrease in reproductive success is likely a delayed consequence of reduced investment at the laying stage rather than behavioral changes during offspring rearing.

Surprisingly, reproductive responses to nest predation risk did not vary with life-history pace. Although species with a slow life-history pace are expected to be sensitive to adverse breeding conditions (Roff 1993, Erikstad et al. 1998), our results suggest that phenotypic responses to a high nest predation risk at the time of egg-laying do not differ along a life-history spectrum. Furthermore, we found no relationship between natural predation rates and responses to an artificially increased perceived risk, despite that the few studies which have addressed variation in responses to risk have largely focused on differences in evolutionary histories of predation pressure (Lima and Dill 1990, Relyea 2001, Ghalambor et al. 2013; but see LaManna and Martin 2016). Nevertheless, interspecific differences in clutch size and volume were significantly related to natural predation rates, suggesting that mean levels of predation risk impact the evolution of reproductive strategies but do not influence responses to variation in risk in ecological time. This result corroborates recent claims that risk-dependent reproductive decisions may have a proportionally higher impact on reproductive success in species with generally low predation rates (Creel and Christianson 2008, LaManna and Martin 2016).

In conclusion, our results illustrate that predation risk is an important selective factor influencing avian reproductive decisions among species, yet the mechanisms and consequences of this influence require further attention. In particular, the novel link between within-clutch egg size variation and predation risk highlights that family-living species may use a bet-hedging strategy under high risk conditions. Furthermore, increased nest predation risk at the time of egg-laying had delayed detrimental effects on reproductive success, emphasizing the need for assessment of how variable risk levels at different times during the breeding cycle ultimately affect reproductive success. Finally, these results further demonstrate that responses to nest predation risk prior to breeding are not "one size fits all" among species, and accentuate the need for additional comparative studies to understand the evolved mechanisms for coping with changes to offspring predation risk and to develop a framework of how other life-history, ecological and/or social factors contribute to interspecific differences.

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3.6 Supplementary Material

Table S1. Correlation matrix, standardized principal components loadings, and communality (h^2) of continuous species traits. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix					loadings		h^2
	body mass	time in nest	time post-fledging	adult survival	PC1	PC2	
body mass	1	0.58	-0.39	0.95	**0.93**	-0.25	0.98
time in nest (laying – fledging)	0.58	1	0.14	0.53	**0.82**	0.44	0.78
time post-fledging	-0.39	0.14	1	-0.16	-0.09	**0.95**	0.93
adult survival	0.95	0.53	-0.16	1	**0.93**	-0.07	0.88
eigenvalue					2.44	1.13	
cumulative variance explained (%)					60	89	

Table S2. Odds ratios (OR) and corresponding 95% credible intervals (C.I.) and p-values (p) for predictors of nest failure at the egg stage, nestling stage, and overall nest failure. Significant fixed effects (p<0.10) are denoted in bold. Random effects are variance and respective 95% credible intervals.

	failure at egg stage				failure at nestling stage				overall nest failure			
	OR	95% C.I. lower	95% C.I. upper	p	OR	95% C.I. lower	95% C.I. upper	p	OR	95% C.I. lower	95% C.I. upper	p
fixed effects												
intercept[1]	0.07	0.01	2.14	0.01	**0.01**	**0.00**	**0.05**	**<0.01**	**0.07**	**0.02**	**0.36**	**<0.01**
treatment (predator)[2]	0.74	0.25	2.18	0.59	**3.74**	**1.15**	**12.43**	**0.01**	**2.20**	**1.07**	**5.37**	**0.06**
life history pace	1.36	0.61	2.94	0.40	0.53	0.18	1.40	0.19	0.77	0.39	1.35	0.36
time post-fledging	0.84	0.36	2.08	0.67	0.98	0.45	2.08	0.95	0.84	0.50	1.40	0.51
number of clutches	**2.34**	**0.93**	**6.23**	**0.08**	1.27	0.41	5.16	0.67	1.51	0.69	3.29	0.28
predation risk	0.99	0.95	1.03	0.53	**1.08**	**1.05**	**1.12**	**<0.01**	**1.06**	**1.02**	**1.09**	**<0.01**
nest type (open)[2]	0.30	0.06	1.42	0.12	2.10	0.42	9.58	0.34	1.52	0.54	4.53	0.44
laying date	1.02	0.97	1.06	0.42	0.98	0.92	1.04	0.57	1.01	0.97	1.04	0.67
predator (mammalian)[2]	1.28	0.21	7.77	0.77	0.54	0.10	3.03	0.48	0.91	0.29	3.32	0.87
proximity to nest	1.30	0.57	2.53	0.50	1.01	0.52	1.97	0.96	1.08	0.67	1.75	0.73
treatment (predator) x nest type (open)	**6.82**	**0.89**	**48.42**	**0.03**								
random effects												
Species	0.18	0.0003	0.65		0.30	0.0003	1.22		0.08	0.0002	0.35	
Year	0.25	0.0002	1.10		8.06	0.0003	25.33		0.16	0.0002	0.89	

[1] The reported intercepts correspond to reduced models.

[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an odds ratio (OR) of 1.

Table S3. Correlation matrix, standardized principal components loadings, and communality (h^2) of continuous species traits excluding Siberian jays. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix					loadings		h^2
	body mass	time in nest	time post-fledging	adult survival	PC1	PC2	
body mass	1	0.59	-0.46	0.95	**0.93**	-0.26	0.99
time in nest (laying – fledging)	0.59	1	0.14	0.52	**0.84**	0.49	0.84
time post-fledging	-0.46	0.14	1	-0.28	-0.14	**0.93**	0.92
adult survival	0.95	0.52	-0.28	1	**0.91**	-0.15	0.89
eigenvalue					2.43	1.21	
cumulative variance explained (%)					0.61	0.91	

Table S4. Model estimates and corresponding standard errors and p-values for predictors of allocation into eggs, excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est.=estimate, p=p-value.

	egg volume			clutch volume			egg volume variation		
fixed effects	est.	SE	p	est.	SE	p	est.	SE	p
intercept[1]	0.07	0.16	0.66	-0.002	0.29	0.99	-0.10	0.19	0.62
treatment (predator)[2]	0.003	0.02	0.87	**-0.06**	**0.03**	**0.03**	**0.25**	**0.15**	**0.09**
life-history pace	**0.81**	**0.16**	**<0.01**	**1.13**	**0.34**	**0.03**	0.01	0.21	0.95
time post-fledging	-0.23	0.16	0.21	0.27	0.53	0.65	-0.05	0.22	0.83
number of clutches	**0.27**	**0.11**	**0.08**	0.63	0.34	0.13	-0.23	0.21	0.33
predation risk	0.06	0.05	0.30	-0.03	0.07	0.76	0.12	0.18	0.62
nest type (open)[2]	-0.001	0.30	0.99	-0.54	0.70	0.50	-0.44	0.41	0.34
laying date	**-0.02**	**0.01**	**0.07**	**-0.07**	**0.02**	**<0.01**	-0.09	0.09	0.32
predator type (mammalian)[2]	-0.02	0.41	0.96	0.57	0.66	0.45	-0.42	0.55	0.49
proximity to nest	0.05	0.04	0.26	0.01	0.02	0.64	**-0.30**	**0.10**	**<0.01**
clutch size	0.02	0.02	0.16	**0.34**	**0.02**	**<0.01**	0.07	0.12	0.54
treatment (predator)[2] x number of clutches				**-0.06**	**0.03**	**0.03**			
treatment (predator)[2] x time post-fledging							**0.49**	**0.17**	**<0.01**
random effects									
species	0.41			0.75			0.43		
year	<0.01			<0.01			<0.01		
nest	0.10								

[1] Reported intercepts are from reduced models, which include only the fixed effects in bold.
[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table S5. Model estimates and corresponding standard errors and p-values for predictors of the number of offspring at each nest stage excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are standard deviation. est. =estimate, p=p-value.

	clutch size			number of nestlings			number of fledglings		
fixed effects	**est.**	**SE**	**p**	**est.**	**SE**	**p**	**est.**	**SE**	**p**
intercept[1]	**1.69**	**0.06**	**<0.01**	**1.42**	**0.06**	**<0.01**	**1.31**	**0.08**	**<0.01**
treatment (predator)[2]	-0.04	0.07	0.61	0.06	0.09	0.46	0.13	0.12	0.28
life-history pace	**-0.13**	**0.06**	**0.04**	0.04	0.04	0.31	0.07	0.05	0.15
time post-fledging	-0.05	0.07	0.41	0.04	0.06	0.44	0.05	0.07	0.50
number of clutches	**-0.22**	**0.06**	**<0.01**	-0.07	0.06	0.20	-0.12	0.08	0.12
predation risk	**0.15**	**0.07**	**0.02**	<0.01	0.05	0.98	0.05	0.08	0.58
nest type (open)[2]	**-0.35**	**0.12**	**<0.01**	0.03	0.10	0.79	0.13	0.17	0.45
laying date	-0.01	0.04	0.73	-0.03	0.05	0.59	-0.01	0.06	0.90
predator type (mammalian)[2]	-0.08	0.10	0.41	0.02	0.10	0.86	<0.01	0.13	0.96
proximity to nest	<0.01	0.05	0.99	-0.05	0.05	0.29	<0.01	0.06	0.99
clutch size	na	na	na	**0.35**	**0.05**	**<0.01**	**0.20**	**0.07**	**<0.01**
random effects									
species	<0.01			<0.01			<0.01		
year	<0.01			<0.01			<0.01		

[1] Reported intercepts are from reduced models, which include only the fixed effects in bold.
[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an estimate of 0.

Table S6. Odds ratios (OR) and corresponding 95% credible intervals (C.I.) and p-values (p) for predictors of nest failure at the egg stage, nestling stage, and overall nest failure, excluding Siberian jays. Significant fixed effects (p<0.10) are denoted in bold. Random effects are variance and respective 95% credible intervals.

	failure at egg stage				failure at nestling stage				overall nest failure			
	OR	**95% C.I. lower**	**upper**	**p**	**OR**	**95% C.I. lower**	**upper**	**p**	**OR**	**95% C.I. lower**	**upper**	**p**
fixed effects												
intercept[1]	0.66	0.16	2.27	0.55	**0.13**	**0.04**	**0.33**	**<0.01**	0.61	0.31	1.16	0.14
treatment (predator)[2]	0.77	0.28	2.32	0.64	**3.56**	**1.19**	**13.60**	**0.03**	**1.99**	**0.90**	**5.10**	**0.09**
life history pace	0.73	0.37	1.54	0.31	0.53	0.18	1.62	0.23	0.76	0.41	1.40	0.32
time post-fledging	0.93	0.34	2.29	0.88	0.64	0.19	1.97	0.40	0.84	0.43	1.67	0.59
number of clutches	**0.96**	**0.91**	**1.01**	**0.09**	1.48	0.54	4.14	0.36	1.32	0.73	2.44	0.34
predation risk	1.79	0.61	5.53	0.25	**4.66**	**2.44**	**10.49**	**<0.01**	**2.69**	**1.42**	**4.90**	**<0.01**
nest type (open)[2]	0.59	0.09	3.71	0.59	2.12	0.26	21.76	0.47	2.27	0.58	8.85	0.19
laying date	1.02	0.99	1.06	0.26	0.73	0.30	1.60	0.47	1.06	0.66	1.63	0.81
predator (mammalian)[2]	1.54	0.27	8.00	0.50	0.60	0.09	4.90	0.60	0.88	0.24	3.35	0.83
proximity to nest	3.74	0.68	21.76	0.14	0.76	0.41	1.39	0.40	0.80	0.20	3.86	0.77
treatment (predator) x nest type (open)	**19.89**	**2.29**	**202.35**	**<0.01**								
random effects												
species	0.32	0.001	1.14		0.39	0.002	1.70		0.19	0.002	0.71	
year	1.66	0.002	6.09		25.8	0.004	85.44		0.66	0.002	1.75	

[1] The reported intercepts correspond to reduced models.
[2] Reference levels of categorical variables (i.e. control group, closed nests, and avian predator) have an odds ratio (OR) of 1.

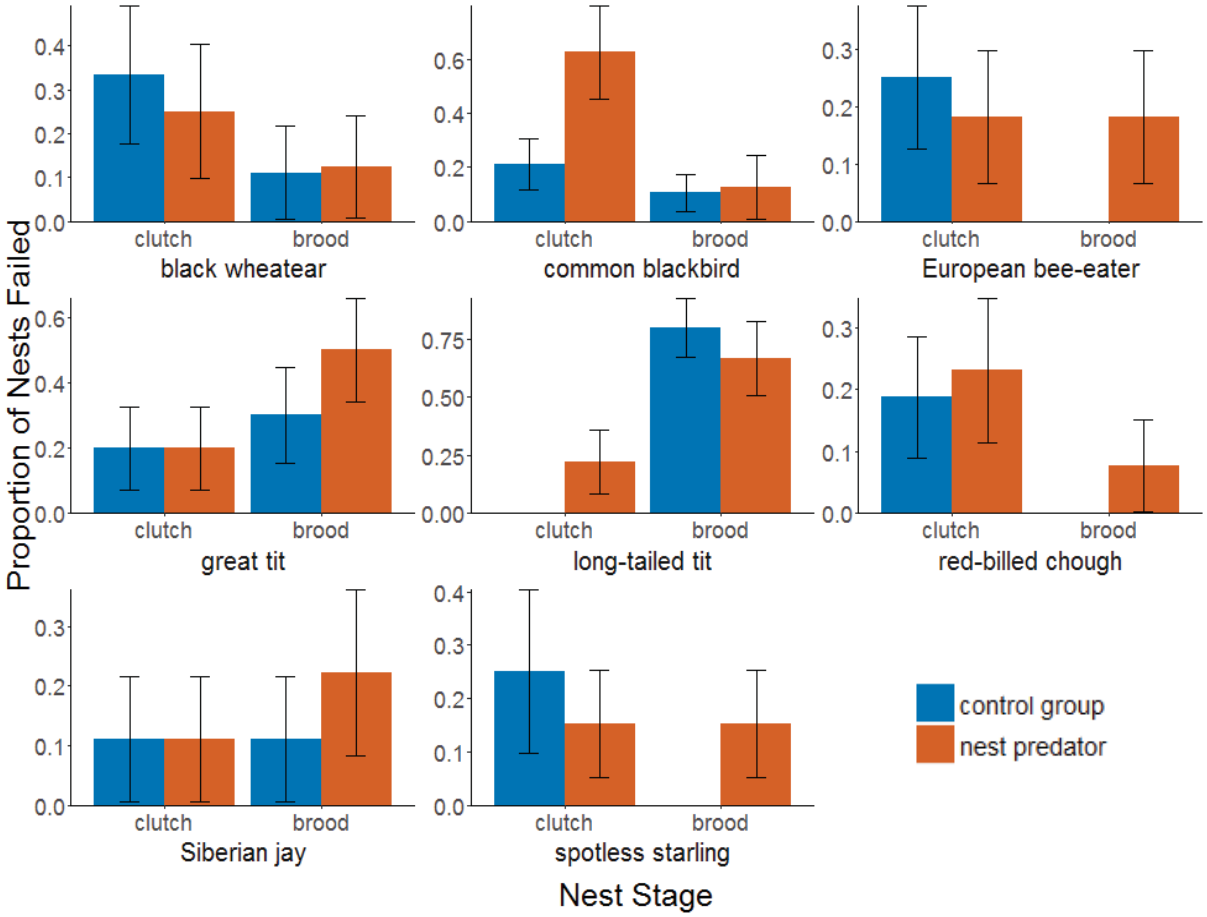

Figure S1. Nest failures (proportion failed +/- SE) at the egg stage and the nestling stage per treatment

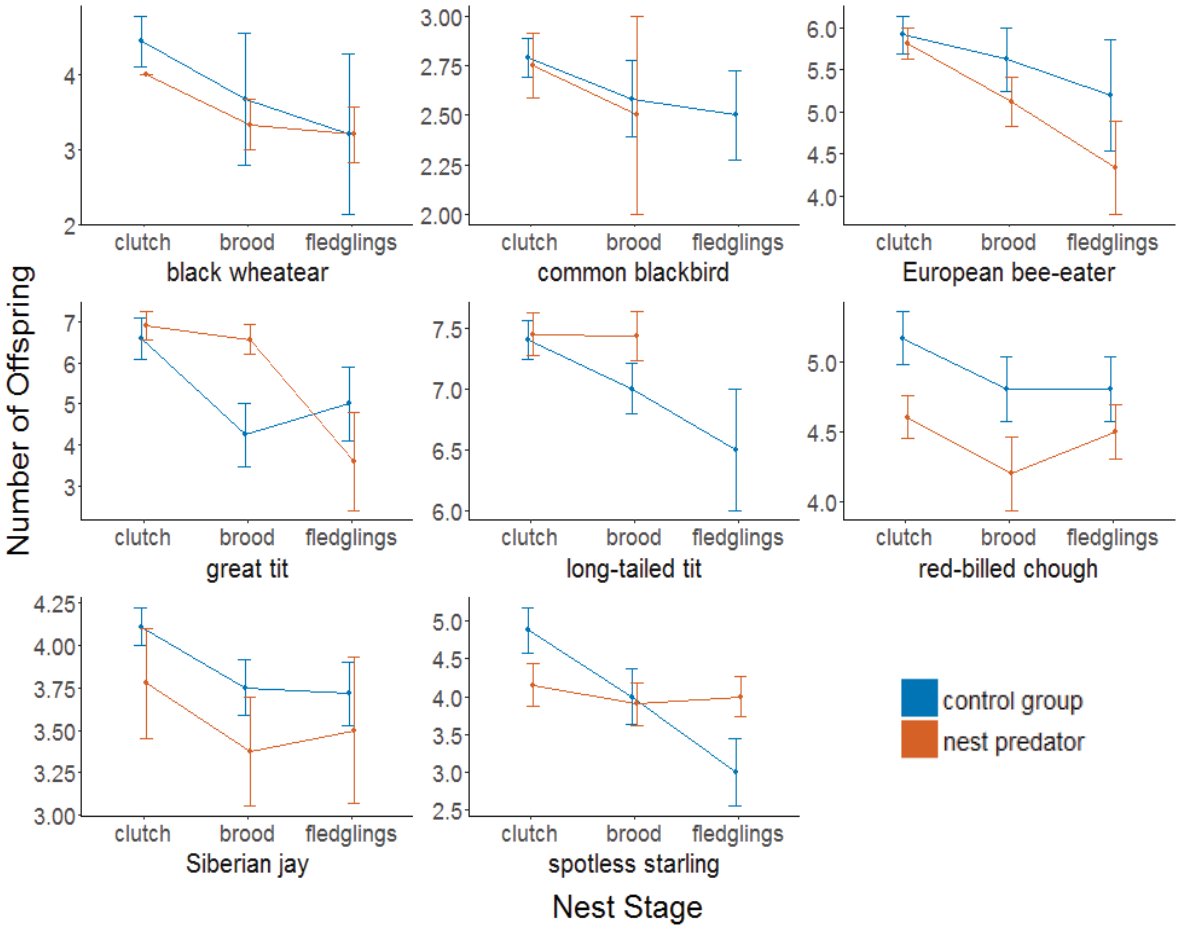

Figure S2. The number of eggs, nestlings and fledglings per treatment for each species, including only the nests that succeeded in the respective phase.

Chapter 4

Reproductive trade-offs in a long-lived bird species: condition-dependent reproductive allocation maintains female survival and offspring quality

Michael Griesser [1, 2], Gretchen F Wagner [1, 2], Szymon M Drobniak [1,3], Jan Ekman [4†]

[1] Department of Anthropology, University of Zürich, Zürich, Switzerland
[2] Institute of Ecology and Evolution, University of Bern, Bern, Switzerland
[3] Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland
[4] Department of Ecology and Genetic/Population Biology and Conservation Biology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden
[+] deceased

4.1 Abstract

Life-history theory is an essential framework to understand the evolution of reproductive allocation. It predicts that individuals of long-lived species favour their own survival over current reproduction, leading individuals to refrain from reproducing under harsh conditions. Here we test this prediction in a long-lived bird species, the Siberian jay *Perisoreus infaustus*. Long-term data revealed that females rarely refrain from breeding, but lay smaller clutches in unfavourable years. Neither offspring body size, female survival nor offspring survival until the next year was influenced by annual condition, habitat quality, clutch size, female age, or female phenotype. Given that many nests failed due to nest predation, the variance in the number of fledglings was higher than the variance in the number of eggs and female survival. An experimental challenge with a novel pathogen before egg-laying largely replicated these patterns in two consecutive years with contrasting conditions. Challenged females refrained from breeding only in the unfavourable year, but no downstream effects were found in either year. Taken together, these findings demonstrate that condition-dependent reproductive allocation may serve to maintain female survival and offspring quality, supporting patterns found in long-lived mammals. We discuss avenues to develop life-history theory concerning strategies to offset reproductive costs.

4.2 Introduction

Life-history theory is an essential framework to understand the evolution of allocation of resources into reproduction and survival (Williams 1966, Stearns 1992). It predicts that individuals have to trade off the allocation of their finite resources (van Noordwijk and de Jong 1986) and accordingly, reproductive allocation in a given event correlates negatively with the expected lifespan of an individual (Williams 1966, Stearns 1992). Since long-lived species invest in somatic maintenance (i.e., survival) rather than reproduction, variance in adult survival has been shown to be smaller than variance in reproductive allocation (Gaillard et al. 2000, Hamel et al. 2010). Consequently, their reproductive decisions are predicted to be sensitive to limitations in resource availability due to environmental stochasticity.

Field studies support the idea that long-lived species generally invest less into reproduction than short-lived species (Stearns 1992, Hamel et al. 2010, Mourocq et al. 2016), and may refrain from reproduction under unfavourable conditions, i.e., exhibit intermittent breeding (Shaw and Levin 2013). Intermittent breeding is most commonly reported in long-lived species that breed in temporally variable environments (Bradley et al. 2000, Covas et al. 2004). However, clutch or brood size manipulations, the main techniques used to assess reproductive trade-offs in egg laying species (Dijkstra et al. 1990, Santos and Nakagawa 2012), generally exclude individuals that exhibit intermittent breeding in the experimental season. Thus, we may systematically underestimate the extent of adjustments to reproductive allocation in long-lived species.

A number of experiments in birds did manipulate the conditions prior to breeding. They showed that food-supplemented females increase their reproductive allocation (Gasparini et al. 2007, Kerr et al. 2007, Karell et al. 2008, Parejo et al. 2012), while food-deprived females produce low quality offspring (Gorman and Nager 2004). Also, females increase clutch size, egg mass and feeding rate when predators are removed (Fontaine and Martin 2006), but reduce clutch size under increased perceived predator abundance (Eggers et al. 2006). Yet, food and predator abundance manipulations may affect multiple aspects of an individual's reproductive decisions in natural populations, calling for experiments that specifically manipulate female condition before egg-laying.

Here we investigate the association between reproductive allocation, survival and offspring quantity and quality, using longitudinal and experimental data from a natural population of Siberian jays, *Perisoreus infaustus*. This open-nesting bird species is long-lived (maximum lifespan of Siberian jays=17.9 years; average maximum lifespan of N=1128 bird species: 14.4 years; Valcu et al. 2014). Most females make one annual breeding attempt, laying 1-5 eggs, with re-nesting occurring in 3.1% of breeding attempts. However, they rarely refrain from breeding under unfavourable conditions (Eggers et al. 2006). Previous work in the study population revealed that females adjust their reproductive allocation depending on the perceived predation risk and habitat quality, and the interplay between these two factors determines their reproductive output. Females breeding in territories with an increased risk of nest predation (Eggers et al. 2006) and more open territories (Nystrand et al. 2010) have smaller clutches and a lower nesting success. The principal nest predators of Siberian jays (i.e., other corvids) are visual hunters, which locate nests more easily when parents feed a larger brood (Eggers et al. 2006), or when nests are located in more open habitats (Griesser et al. 2007).

Siberian jays live in stable groups composed of a dominant breeding pair (hereafter referred to as breeders, or singly as female or male) and up to four non-breeders. Reproduction is strictly kept within the breeding pair (Ekman and Griesser 2016) and in successful broods, subordinate offspring are evicted by dominant siblings within 1-2 months of fledging (Ekman et al. 2002), after which they disperse to other groups to wait for a breeding opening (hereafter termed early dispersers). Offspring that delay dispersal can remain with their parents up to three years (hereafter termed philopatric individuals; Griesser et al. 2008), acquire territories of higher quality, and have a longer lifespan and a higher lifetime reproductive success than the evicted early dispersers (Ekman and Griesser 2016). Because females that dispersed early have shorter lives than females that delayed their dispersal (Ekman and Griesser 2016), they might face different reproductive trade-offs than females that delayed their dispersal, but this has not yet been tested.

We used long-term data collected over 26 years, including 20 years of detailed data on reproductive allocation, to investigate how females adjust their reproductive allocation depending on i) annual conditions, ii) their dispersal phenotype, and iii) breeding habitat quality. We

measured reproductive allocation by females (number of eggs and fledglings), and assessed costs of reproduction by recording survival until spring of the following year for females and offspring as well as offspring body size and feather quality. Since Siberian jays are a long-lived species, reproductive allocation should show high variance (high allocation in favourable years, low allocation in unfavourable years) but not affect subsequent female survival. Females that delayed their dispersal and those breeding in high-quality habitats are expected to lay larger clutches and/or bigger eggs (van Noordwijk and de Jong 1986, Williams 2001) (leading to more fledglings) than early dispersing females and those breeding in low-quality habitats. Offspring hatching from larger eggs may experience increased survival (Metcalfe and Monaghan 2001, Krist 2011).

To assess reproductive allocation trade-offs experimentally, we used an immune system challenge in two breeding seasons with contrasting weather conditions. We injected females with a novel antigen (*Brucella abortus* suspension; hereafter shortened to BA), a bacterium causing brucellosis in mammals. In birds it does not occur naturally and when administered induces an immune reaction which can be detected for 2-3 weeks through the proliferation of B-cells (Amat et al. 2007). Injecting BA prior to breeding should change the resource allocation of females, and thus BA injected females were expected to i) delay the onset of breeding, ii) lay smaller clutches and/or eggs, or iii) refrain from breeding altogether, particularly in unfavourable years or when breeding in low-quality habitat. Offspring hatching from smaller eggs would be of lower phenotypic quality (Krist 2011), leading to increased mortality during their first year of life (Metcalfe and Monaghan 2001).

4.3 Methods

We collected data for this study from an individually colour-ringed population of Siberian jays in boreal forest habitats near Arvidsjaur, Northern Sweden (65°40’ N, 19°10’ E). We used data on reproductive allocation collected between 1989 and 2014 (n=3-55 territories per year; increase due to enlarged study site) and experimental data collected in the years 2011 and 2012 (n=55 territories). As Siberian jays are sexually monomorphic, we took 50-80µL blood from all birds for

molecular sex determination (Griffiths et al. 1998). All procedures were done under the license of the Umeå ethics board, license number A 80-99, A 45-04 and A 50-11.

Assessment of reproductive allocation, offspring quality and survival

To assess reproductive allocation, we counted the number of eggs and fledglings, measured the adult body size of offspring after fledging, and assessed offspring feather condition (i.e. number of fault bars, see below; Grubb 2006). From 1989 to 2004 and from 2011 onwards we caught females in March and attached a radio-tag (Holohil BD-2D, Telenax TBX-006), to aid with locating the nests. Nests were visited repeatedly to count the number of eggs, nestlings and fledglings, and ring all fledglings (Griesser et al. 2012). We did not follow reproduction between 2005 and 2010, but we could reliably assess whether pairs bred successfully or not (hereafter termed nesting success) based on the presence of delayed dispersing juveniles in autumn (see below). The rank of individuals was based on dominance hierarchies among group members assessed on feeders (see below).

To assess juvenile quality, we caught juveniles 1-3 months after fledging to measure their adult body size and count the number of fault bars in their wing and tail feathers. Fault bars are growth deficiencies visible as translucent bars across feathers, thought to reflect elevated physiological stress levels during feather growth (Grubb 2006). An earlier study in Siberian jays showed that a high number of fault bars was linked to increased overwinter mortality of juveniles (Griesser et al. 2006). Fault bars make feathers more prone to breakage, which in turn reduces manoeuvrability and escape speed during predator attacks (Williams and Swaddle 2003). We surveyed the survival of females and delayed dispersing juveniles until the next spring by repeatedly visiting all groups in early March before the onset of the next breeding season. Earlier studies showed that all 110 individuals that were radio-tagged in autumn either remained in their territory and survived (N=94), or were found dead in the territory, killed by a predator (N=16; Griesser 2013). Moreover, Siberian jay groups are very stable and non-breeders generally only move into breeding openings in neighbour territories later on in spring (Ekman and Griesser 2016).

Assessment of dispersal phenotype (early vs delayed dispersing individuals)

We assessed the dispersal phenotype of individuals using two different methods: either from their life-history, or using a behavioural assessment. In years that we located nests, we recognized delayed dispersing juveniles that remained on the parental territory based on their numbered metal ring. Unringed juveniles settling in groups were consequently classified as early dispersers (Griesser et al. 2008). In years that we did not locate nests, we classified the dispersal phenotype of juveniles using a behavioural assessment on feeders placed in the territory in autumn, following a standardized protocol (Ekman et al. 1994). Breeders are socially dominant over other group members and share a feeder with their own offspring, while they aggressively displace or chase unrelated group members away from a feeder (Griesser et al. 2015). This method is fully reliable when compared with juveniles of known origin (n=120 juveniles: all correctly assigned; Ekman et al. 1994, Griesser 2003). The dispersal timing of individuals that immigrated into the study population after their first winter was unknown, and they were classified with "unknown" dispersal phenotype.

Assessment of habitat quality

The study site has two areas, one dominated by managed forests and the other by unmanaged forests (Griesser et al. 2007). The managed area is located closer to human settlements, and has a higher number of nest predators compared to the unmanaged area (Eggers et al. 2005a). In addition, forests in managed territories are more open and consequently adult birds have a higher risk of being killed by their main predators, accipiter hawks (goshawk *Accipiter gentilis,* sparrowhawk *A. nisus*), than birds living in unmanaged territories (Griesser et al. 2006).

Immunological challenge experiment

We performed an immunological challenge experiment in two breeding seasons with different weather conditions. In 2011, mean spring temperatures (April, May) were 2.7°C warmer than the long-term average and the mean nesting success was the highest (83%) since the onset of fieldwork in our study population in 1989. In 2012, the mean spring temperatures were 0.3°C below average and the mean nesting success (29%; excluding BA injected females) was lower than average (42%). We used a counterbalanced design to assign females with known dispersal

phenotype (*n*=27) to a treatment group (sum over both years: BA: *n*=20, saline: *n*=21), balancing habitat quality (managed, unmanaged forests), and the weighted average of the long-term mean nesting success of the territory relative to all other territories (see Griesser et al. 2007 for detailed description of calculation). We also injected four females of unknown phenotype. Most females of unknown phenotype (*n*=22), along with 5 delayed dispersing females and 5 early dispersing females, were not injected (labelled control hereafter) to have baseline data available for untreated birds (supplementary material Table S1). For females which were injected in both years, we used the reverse treatment in 2012 (*n*=15). We note that the experimental treatment in the first year did not influence the reproductive investment and female survival in the second year (Table S2).

We captured females in March, 13-49 days (mean ± SE: 29.3±2.2 days) before the onset of egg laying (mean long-term onset of egg laying: 6th April) using mist nets or ground nets, attached a radio-tag and injected 100µL BA solution (Veterinary Laboratories Agency, Addlestone, UK) or 100µL sterile saline solution intra-peritoneally, or did not inject anything (controls). The dosage was chosen carefully based on several earlier studies injecting BA solution in birds (Birkhead et al. 1998, Amat et al. 2007, Sild et al. 2011). We chose this time window to ensure that females experienced the effect of the BA injection before the onset of egg laying. We followed females regularly with the help of the radio-tags, until we found their nest. We were unable to locate nests in nine cases, either due to predation of the female (*n*=2) or male (*n*=1; females without males do not nest), or due to radio-tag failure (*n*=6). Once temperatures were warm enough (>5°C) we returned to climb the nest tree to count the number of eggs and measure them with dial callipers (0.1mm accuracy). Nests were visited 2-5 times during the nestling period to measure the nestlings and to ring them with a numbered metal ring and three colour rings. We applied clip marks to claws to identify individual nestlings before ringing.

Statistical analyses

We used ASReml v. 3.0 (Gilmour et al. 2009) in R 3.0.2 (R Core Team 2014) to run linear mixed models (LMM) and generalized linear mixed models (GLMM). The decision whether to use LMM

or GLMM was based on the inspection of residuals on diagnostic plots, except for binary data, where in all cases binomial-error GLMMs were used.

Long-term data:

We tested with a random regression LMM whether annual condition (assessed as the mean proportion of females that fledged at least one offspring in the population), habitat quality, female age and female phenotype affected the number of eggs individual females laid across different years. Defining annual condition in a measurement that integrates the fitness consequences for the organism (e.g., using breeding success as here, or offspring survival as in a study on Soay sheep *Ovis aries* (Robinson et al. 2009)) has been suggested to lead to a composite measure of poor and good annual conditions in a relevant 'currency' (Stinchcombe and Kirkpatrick 2012). Intuitively, average clutch size and the proportion of successfully breeding females in a population could be closely linked due to a statistical artefact. We excluded this possibility using a simple simulation based on the breeding parameters observed in our study population (see additional methods). The average clutch size and annual mean nesting success could be correlated when nests with a small clutch size are more likely to fail than nests with a larger clutch size. Given that females do not initiate a clutch only in exceptional cases, we excluded these cases from the simulation. The simulation showed that the correlation between the two quantities cannot arise due to statistical sampling and mathematical artefacts, supporting the biological value of the mean annual nesting success.

We excluded nests of females that were experimentally challenged with BA in 2012, nests of females that were exposed to predator playbacks (Eggers et al. 2006), and females that lacked a mate (see above). We included female identity as a random factor to control for the repeated use of the same females in subsequent years. Random slopes enabled additional variation in the steepness of relationships between reproductive allocation and annual condition across individual females. We used the same type of model and independent variables to investigate the influence of annual condition on the number of fledglings. We used GLMMs (binomial error structure, logit link function) to assess the influence of whether females bred successfully or not, number of eggs,

habitat quality, female age and female phenotype on female survival until the following year, including territory and year as random factors.

To assess offspring adult body size and feather quality, we first ran principal component analyses to reduce bivariate, co-linear data into single variables. Given that a higher number of fault bars corresponds to low feather quality, we multiplied the number of fault bars by -1, so that a higher number corresponds to high feather quality. The PCA for body size included tarsus length and wing length; the PCA for feather quality included the maximum numbers of fault bars in wing and tail feathers. In both PCAs the first PC respectively explained 77% and 71% of the variance and thus, only the first PCs were used as response variables in subsequent models (Table S3). We analysed these data using LMMs including annual condition, female age and phenotype, habitat quality and the number of siblings on offspring feather quality and offspring adult body size, including territory and year as random factors.

We investigated whether the mean-standardized measures of within-year variance (coefficients of variation, calculated from raw data) in reproductive and quality traits of individuals differed. We used a Kruskal-Wallis test due to lack of both normality and homogeneity of variance between different types of traits. Variances were calculated assuming appropriate distribution of the original data. For the number of eggs and fledglings we assumed Poisson distribution, and thus *variance = mean*, and for female and offspring survival we assumed binomial distribution, and thus *variance = mean*(1-mean)*.

Experimental data:

Data on reproductive allocation of females were analysed using general linear mixed models in a repeated measures framework. We included female investment as a response variable in the model, measured as the number of eggs, nestlings and fledglings at the respective stage of the breeding cycle. Accordingly, the investment was treated as a repeated measure and the repetition level was the stage of the cycle, included in the model as a fixed categorical variable. We included the following fixed effects in the model: experimental treatment (categorical variable: BA/saline/control), year (categorical variable: 2011/2012), habitat quality (categorical variable:

managed/unmanaged forest), female phenotype (categorical variable: kin/non-kin/unknown), female age (continuous) and the time difference between BA injection and egg laying for each female (continuous variable). To account for possible repeated measurements of individuals (N=27 females were studied in both years), we included female identity as a random categorical variable. In our framework, estimates of the stage variable provide a means to assess the change in female investment over the course of the reproductive cycle, and its interaction with treatment shows how much the rates of these changes vary across the experimental groups.

We investigated the association between our treatment and whether females initiated a clutch or not, or abandoned their brood or not, with Fisher's exact tests. We tested for differences in the volume of individual eggs (calculated following Hoyt 1979) using a LMM, including nest identity as a random factor. We tested the influence of the treatment on offspring adult body size and feather quality using a LMM (*n*=83 offspring), while female survival until the next year, and survival of delayed dispersing juveniles until the next year (*n*=83 offspring) were analysed using GLMMs (binomial error structure, logit link function). In all models testing offspring parameters, we included female identity as random factor to control for the fact that we sampled several offspring of the same female.

We included the following measurements as independent variables in all models assessing experimental data: injection treatment (BA, saline, control), number of days between catching the females to inject them (or not in case of the control females) and median egg laying date of the year, habitat quality (managed *vs.* unmanaged), year (2011 vs. 2012) and female phenotype (early disperser, delayed disperser, unknown). We used the median egg laying date instead of the actual egg laying date given that in 2012 most BA injected females did not attempt to breed (see below). In models assessing offspring size, quality and survival, we also included the number of siblings in the models.

4.4 Results

Long-term data

The annual mean number of eggs varied between 0.75 and 3.98 across years (mean±SE=3.29±0.19), and was higher in years with a high mean nesting success (i.e., a high proportion of successful broods) than in years with a low mean annual nesting success (Fig. 1a, Table 1a). Out of 328 surveyed breeding attempts (N=166 females), females did not initiate a clutch and skipped breeding only in five attempts, and these events were associated with adverse weather conditions during spring in 1997 (*n*=2), an experimental increase of the perceived nest predation risk (*n*=2, excluded from the statistical analyses; Eggers et al. 2006), or low female condition (*n*=1). Also, older females and those breeding in unmanaged habitat laid larger clutches than younger females and those breeding in managed habitat (Table 1a). A lower number of eggs *per se* did not lead to a lower nesting success, as partial nest predation was rare (*n*=1 out of 66 depredated nests) and all nests with infertile eggs also contained fertile eggs that hatched (*n*=76 nests). Rather, nests were either successful (*n*=209) or they failed due to nest predation (*n*=66), predation of a breeder (*n*=7), were abandoned (*n*=12), or the nest failure reason could not be determined (*n*=34). The annual mean number of fledglings varied between 0 and 3.60 across years (mean±SE=1.75±0.09; Fig. 1b), and more nestlings fledged in favourable years than unfavourable years (Table 1b).

In favourable years (i.e., with a high mean nesting success) offspring had a higher feather quality than in years with a low mean nesting success, and offspring of older females and those from larger broods had lower feather quality (*n*=249 offspring; Table 1c). However, adult body size of offspring did not vary across years (*n*=332 offspring; Table 1d; Fig. 2), and no factor was found to influence survival of delayed dispersing offspring until the next spring (*n*=360 offspring; Table 1e). Older females had a lower survival until the next spring than younger females but no other factor was found to influence female survival (*n*=243 females, 758 observations; Table 1f).

The variance of the number of fledglings was larger than the variance of the number of eggs and the survival of females until the next year, but did not differ among the other factors (Fig. 3; pairwise Kruskal-Wallis corrected for multiple comparisons; no. of fledglings vs. no. of eggs: p=0.0002, no. of fledglings vs. female survival: p=0.0004, all other comparisons: p>0.10).

Table 1: Linear mixed models and generalized linear mixed models investigating the factors affecting the number of eggs (a) and fledglings (b), offspring feather quality (c) and body size (d), and female and offspring survival until next year (e and f) in Siberian jays using longitudinal data. The factor "nest failure reason" was included to control for the number of eggs and fledglings independent of nest failure. Significant factors highlighted in bold. den. *df*: denominator degree of freedom; *F*: conditional *F*-statistic; effect sizes: estimates from linear models, for categorical variables expressed as contrasts with the reference category (i.e., treatment contrasts in *R*); *Z* ratio = effect size/SE. imm: immigrant females, philop: philopatric females, unkn: unknown female dispersal phenotype, man: managed habitat, unman: unmanaged habitat, suc: successful reproduction, pred: nest depredated, other: other reason of nest failure.

Model Factor	*df*	den. *df*	*F*	*p*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
a: number of eggs								
intercept	1	143.60	3650	**<0.00001**		2.37	0.23	10.28
female age	**1**	**240.50**	**9.83**	**0.0009**		0.08	0.02	3.36
female dispersal phenotype	2	130.10	0.12	0.68	imm v. philop	0.05	0.19	0.24
					imm v. unkn	-0.09	0.14	-0.63
annual condition	**1**	**81.00**	**24.75**	**0.00001**		1.49	0.32	4.61
habitat	**1**	**121.50**	**4.64**	**0.032**	man v. unman	0.29	0.13	2.16
nest failure reason	1	233.80	0.81	0.37	suc v. failed	0.11	0.12	0.90
b: number of fledglings								
intercept	1	277.00	1118	0.18		-0.61	0.19	-3.14
female age	**1**	**285.90**	**0.67**	**0.013**		0.06	0.02	2.50
female dispersal phenotype	2	186.20	5.41	0.94	imm v. philop	0.02	0.17	0.09
					imm v. unkn	-0.03	0.13	-0.25
annual condition	**1**	**283.10**	**142.70**	**0.0008**		0.97	0.29	3.39
habitat	1	187.80	0.16	0.62	man v. unman	0.06	0.12	0.50
nest failure reason	**1**	**278.80**	**695.70**	**<0.00001**	suc v. failed	2.88	0.11	26.38
c: offspring feather quality								
intercept	**1**	**69**	**8.85**	**0.004**		-1.72	0.66	-2.59
female age	**1**	**69**	**5.54**	**0.02**		-0.12	0.05	-2.35
female dispersal phenotype	2	69	0.11	0.9	philop v. imm	0.13	0.34	0.39
					philop v. unkn	0.02	0.32	0.07
annual condition	**1**	**69**	**27.46**	**<0.00001**		3.42	0.65	5.24
habitat	1	69	0.0085	0.93	man v. unman	0.02	0.25	0.09
number of siblings	**1**	**69**	**7.01**	**0.01**		-0.33	0.12	-2.65
d: offspring body size								
intercept	**1**	**44.1**	**4.36**	**0.04**		-1.81	0.8	-2.26
female age	1	44.4	0.94	0.34		0.06	0.06	0.97
	2	57.3	2.62	0.08	philop v. imm	0.86	0.4	2.16

Model Factor	*df*	den. *df*	*F*	*p*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
female dispersal phenotype					philop v. unkn	0.34	0.39	0.87
annual condition	1	67.6	3.26	0.08		1.37	0.76	1.8
habitat	1	32.1	0.07	0.79	man v. unman	-0.08	0.29	-0.27
number of siblings	1	41.3	0.12	0.72		0.05	0.15	0.35
e: offspring survival								
intercept	1	37.1	2.16	0.15		1.72	1.5	1.15
female age	1	32.7	0.39	0.54		-0.06	0.1	-0.62
female dispersal phenotype	2	49.3	0.06	0.94	philop v. imm	-0.04	0.7	-0.06
					philop v. unkn	0.16	0.71	0.23
annual condition	1	76	0.13	0.72		-0.52	1.45	-0.36
habitat	1	25.7	0.27	0.61	man v. unman	0.27	0.52	0.52
number of siblings	1	33.8	0.22	0.64		-0.13	0.27	-0.46
f: female survival								
intercept	**1**	**304.00**	**81.82**	**0.0002**		2.00	0.60	3.34
female age	**1**	**159.50**	**4.46**	**0.019**		-0.15	0.06	-2.36
female dispersal phenotype	2	92.50	1.29	0.27	imm v. unkn	0.15	0.32	0.46
					imm v. philop	0.84	0.52	1.62
annual condition	1	304.00	0.02	0.63		-0.39	0.82	-0.48
habitat	1	86.30	0.49	0.46	man v. unman	0.25	0.34	0.75
nesting success	1	304.00	1.31	0.25	succ v. failed	-0.36	0.31	-1.14

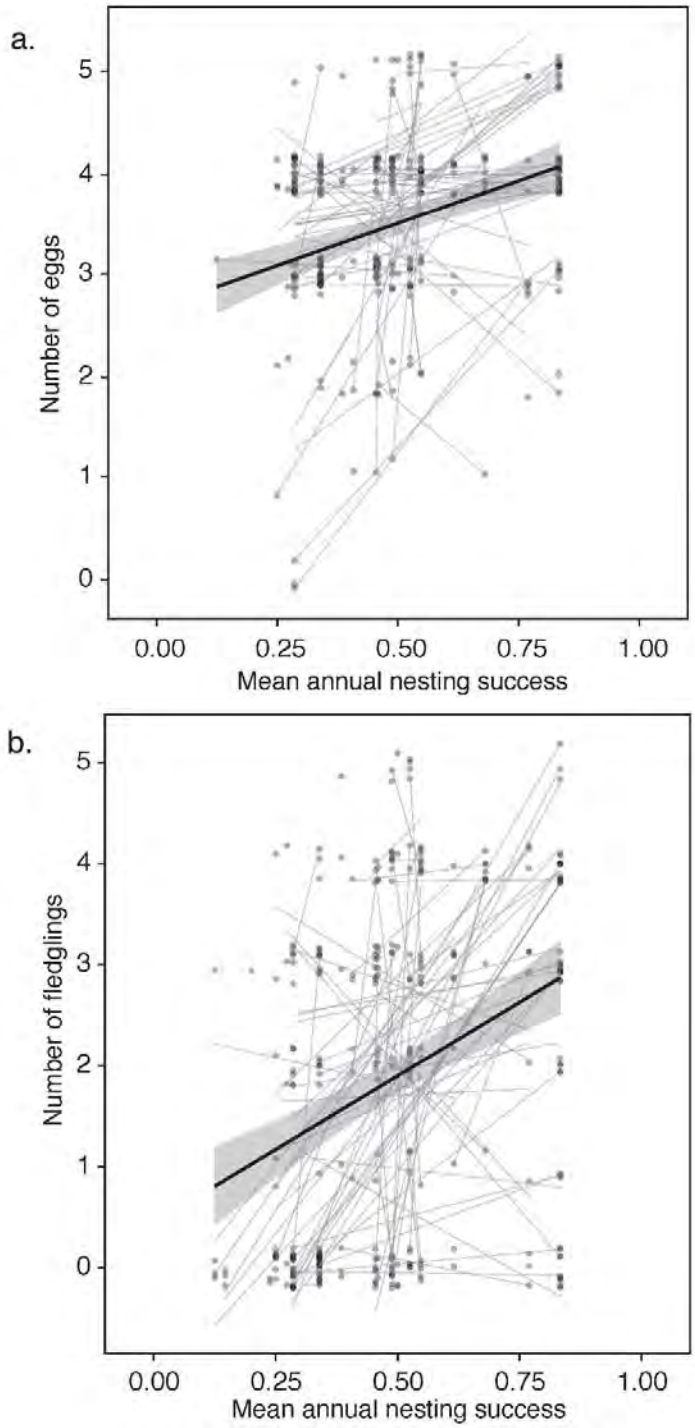

Figure 1. Individual changes in number of eggs (a) and number of fledglings (b) depending on mean annual nesting success. Grey lines: regression slopes for individual females; black line: population-level slope (with its 95% credibility interval indicated by the grey area), for number of eggs: marginal regression slope = 1.47, $p < 0.001$, for number of fledglings: marginal regression slope = 2.94, $p < 0.001$. For clarity the original data points are jittered around their exact values along the Y-axis to make overlapping points visible.

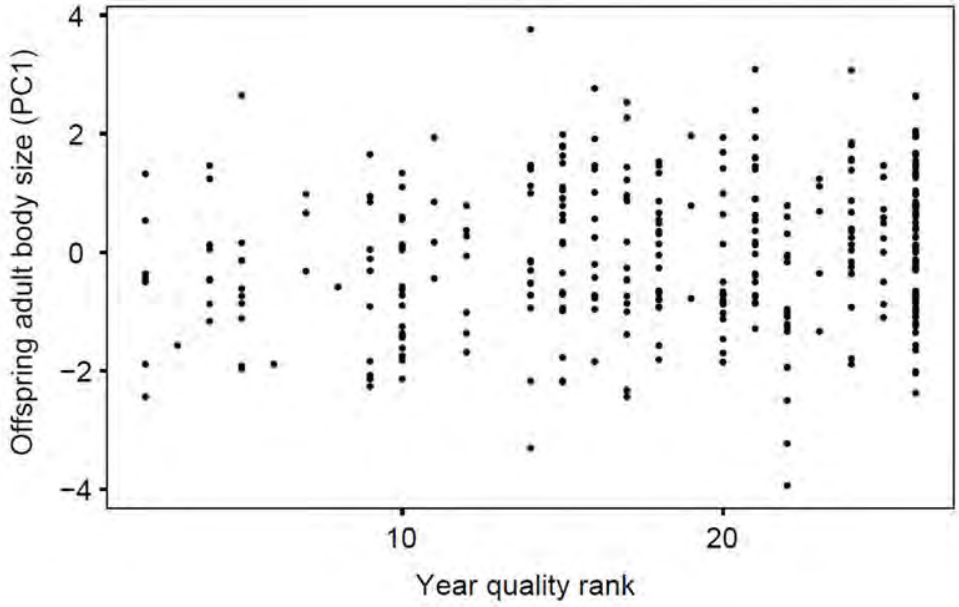

Figure 2: Variation in offspring adult body size across years (1989-2013). Ordered according to quality of the year (i.e., the mean nesting success in the study population). Adult body size of offspring was independent of mean annual nesting success (see Table 1).

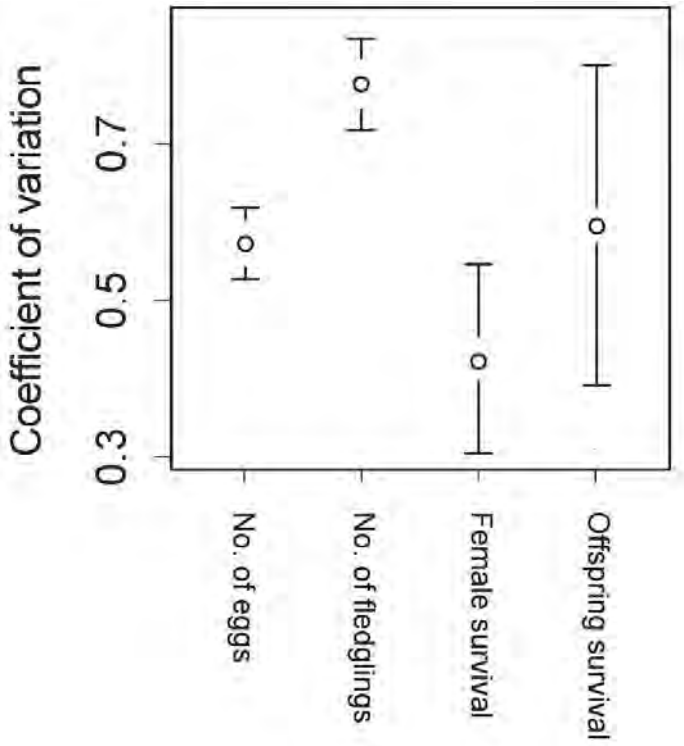

Figure 3. Variance of the number of eggs, the number of fledglings, female survival and offspring survival across all years. The variance of the number of fledglings is significantly higher than for the number of eggs and female survival.

Immunological challenge experiment

The onset of egg laying was earlier in the favorable year (2011) than in the unfavorable year (2012) (GLMM: Wald test $_{df=1}$ = 166.0, p <0.00001), but did not differ between BA and saline injected females (GLMM: Wald test $_{df=2}$ = 1.1, p =0.33). The timespan between catching a female and the median annual laying date was controlled for and did not influence the conclusions regarding experimental effects (Table 2a-c). BA injections were only associated with a lower number of eggs in 2012 (Fig. 4-5; Table 2a), when five out of 12 BA injected females did not initiate a clutch (Fig. 4; Fisher exact test combining both years: p=0.0012), and another three BA injected females abandoned their nest during the egg stage (Fig. 4). Thus, BA injected females laid fewer eggs than saline injected or untreated females (Fig. 4-5, Table 2a). The volume of individual eggs was significantly larger in 2011 than in 2012, and BA injected females laid smaller eggs than saline injected females (Fig. 5, Table 2c). Accordingly, the total number of nestlings and fledglings was higher in 2011 than in 2012, and BA injected females had fewer nestlings and fledglings (Fig. 4-5). The lower number of nestlings and fledglings of BA injected females was not a consequence of increased nest predation rates, which did not differ between the treatment groups (Fishers exact test p=0.30; Table 2b).

Most BA injected females elected to skip breeding or abandoned their clutch soon after egg laying in 2012. Thus, it was not possible to assess the effect of BA injections on the full-grown body size of offspring and their condition under unfavorable conditions. In 2011, no factor was associated with full-grown body size (Fig. 5, Table 2d). In 2012, feather quality correlated negatively with the number of siblings in the brood (Fig. 5, Table 2e), yet survival of delayed dispersing offspring until the following spring was not affected by any factor (n=83 offspring; Fig. 5, Table 2f). BA injected females did not differ in their survival until the following spring compared to saline injected or untreated females (Fig. 5, Table 2g).

Table 2: Linear mixed models (LMM) and generalized linear mixed models (GLMM) investigating the influence of an experiment that immunologically challenged Siberian jay females ahead of egg laying with *Brucella abortus*, saline solution or no treatment. Models assessed the influence of the experimental treatment and year (2011: favorable year, 2012: unfavorable year) on reproductive allocation (number of eggs, nestlings, fledglings; a), reproductive allocation excluding nest that failed due to nest predation (b), egg volume (c), offspring body size (d) and feather quality (e), and female and offspring survival until the next year (f, g). Significant factors highlighted in bold. den. *df*: denominator degree of freedom; *F*: conditional *F*-statistic; effect sizes: estimates from linear models, for categorical variables expressed as contrasts with the reference category (i.e., treatment contrasts in *R*); *Z* ratio = effect size/SE. imm: immigrant females, philop: philopatric females, unkn: unknown female dispersal phenotype, man: managed habitat, unman: unmanaged habitat, BA: *Brucella abortus* injected females, ctr: control females, sal: saline injected females, stage: phrase of reproductive stage: egg, nestling, fledgling stage.

Model: Factor	*df*	den. *df*	*F*	*p*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
a: reproductive allocation:								
intercept	**1**	**202.0**	**900.90**	**<0.00001**		0.10	0.55	0.18
treatment	2	**202.0**	**2.38**	**0.040**	BA v. ctr	-0.14	0.18	-0.79
					BA v. sal	-0.06	0.19	-0.33
year	**1**	**202.0**	**15.13**	**<0.00001**	2011 v. 2012	-1.47	0.23	-6.40
habitat	1	202.0	2.08	0.06	man v. unman	0.17	0.09	1.88
stage	**2**	**202.0**	**8.38**	**0.0006**	eggs v. nestl.	-0.42	0.22	-1.93
					eggs v. fledglings	-0.51	0.22	-2.28
female phenotype	2	202.0	0.99	0.06	philop v. imm	0.08	0.12	0.66
					philop v. unkn	0.29	0.13	2.25
female age	1	202.0	3.05	0.40		0.01	0.02	0.85
timing injection	**1**	**202.0**	**12.37**	**0.011**		0.03	0.01	2.55
treatment x year	**2**	**202.0**	**6.82**	**0.001**	BA v. ctr x year	0.84	0.25	3.33
					BA v. sal x year	0.93	0.27	3.51
treatment x stage	4	202.0	0.29	0.89	BA v. ctr x eggs v. nestl.	0.20	0.25	0.82
					BA v. sal x eggs v. nestl.	0.10	0.28	0.38
					BA v. ctr x eggs v. fledg.	0.23	0.26	0.90
					BA v. sal x eggs v. fledg.	0.17	0.29	0.61
b: reproductive allocation excluding nest that failed due to nest predation:								
intercept	**1**	**176.0**	**755.10**	**<0.00001**		0.06	0.59	0.10
treatment	**2**	**176.0**	**1.50**	**0.046**	BA v. ctr	-0.09	0.20	-0.44
					BA v. sal	0.01	0.21	0.04
year	**1**	**176.0**	**19.61**	**<0.00001**	2011 v. 2012	-1.85	0.28	-6.65
habitat	1	176.0	0.34	0.32	man v. unman	0.10	0.10	1.01
stage	**2**	**176.0**	**5.20**	**0.006**	eggs v. nestl.	-0.30	0.23	-1.27
					eggs v. fledglings	-0.36	0.24	-1.51
female phenotype	**2**	**176.0**	**1.13**	**0.044**	philop v. imm	0.12	0.12	0.99

Model: Factor	*df*	den. *df*	*F*	*p*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
					imm v. unkn	0.34	0.14	2.45
female age	1	176.0	5.52	0.23		0.02	0.02	1.22
timing injection	**1**	**176.0**	**9.48**	**0.026**		0.03	0.01	2.24
treatment x year	**2**	**176.0**	**9.29**	**0.0001**	BA v. ctr x year	1.18	0.32	3.73
					BA v. sal x year	1.30	0.31	4.17
treatment x stage	4	176.0	0.09	0.99	BA v. ctr x eggs v nestl.	0.10	0.27	0.35
					BA v. ctr x eggs v. fledg.	0.10	0.28	0.38
					BA v. sal x eggs v. nestl.	-0.02	0.30	-0.05
					BA v. sal x eggs v. fledg.	0.03	0.30	0.10
c: egg volume:								
intercept	**1**	**149.5**	**551.60**	**0.00001**		6546.84	377.81	17.33
treatment	**2**	**185.8**	**7.23**	**0.0009**	BA v. ctr	165.66	139.47	1.19
					BA v. sal	-344.59	169.10	-2.04
year	**1**	**167.5**	**13.85**	**0.0003**	2011 v. 2012	-895.72	183.69	-4.88
habitat	1	44.2	2.32	0.14	man v. unman	177.98	116.90	1.52
female phenotype	2	48.5	0.40	0.67	philop v. imm	103.79	154.37	0.67
					imm v. unkn	-9.43	158.40	-0.06
clutch size	1	161.8	0.92	0.34		61.81	64.51	0.96
female age	**1**	**45.9**	**7.00**	**0.01**		59.65	22.54	2.65
timing injection	1	99.2	0.83	0.36		6.28	6.90	0.91
treatment x year	**2**	**112.9**	**7.40**	**0.001**	BA v. ctr x year	592.00	186.54	3.17
					BA v. sal x year	1165.15	302.31	3.85
d: offspring body size:								
intercept	1	29.1	0.48	0.49		-1.88	1.04	-1.81
treatment	2	47.5	1.59	0.21	BA v. ctr	0.67	0.36	1.87
					BA v. sal	0.35	0.45	0.78
year	**1**	**53.6**	**5.89**	**0.02**	2011 v. 2012	-1.42	0.63	-2.27
habitat	1	32.1	0.14	0.71	man v. unman	-0.12	0.31	-0.37
female phenotype	2	31.9	1.08	0.35	philop v. imm	0.46	0.38	1.22
					imm v. unkn	-0.01	0.38	-0.02
female age	**1**	**29.6**	**4.97**	**0.04**		0.13	0.06	2.23
number of siblings	1	30.4	0.28	0.60		0.08	0.15	0.53
timing injection	1	30.5	0.43	0.52		0.01	0.02	0.65
treatment x year	1	64.3	0.54	0.47	ctr v. sal x year	0.70	0.95	0.73
e: offspring feather quality:								
intercept	**1**	**69.0**	**6.54**	**0.01**		1.15	1.16	0.99
treatment	2	69.0	1.07	0.35	BA v. ctr	0.14	0.41	0.34
					BA v. sal	0.15	0.51	0.29
year	**1**	**69.0**	**30.95**	**0.00001**	2011 v. 2012	-4.48	0.71	-6.30
habitat	1	69.0	0.36	0.55	man v. unman	-0.21	0.35	-0.60

Model: Factor	*df*	den. *df*	*F*	*p*	Effect size levels (categorical variables)	Solution	SE	*Z* ratio
female phenotype	2	69.0	0.64	0.53	philop v. imm	-0.44	0.42	-1.06
					imm v. unkn	-0.10	0.42	-0.23
female age	1	69.0	2.03	0.16		-0.09	0.06	-1.42
number of siblings	**1**	**69.0**	**5.29**	**0.02**		-0.39	0.17	-2.30
timing injection	1	69.0	1.00	0.32		0.02	0.02	1.00
treatment x year	**1**	**69.0**	**10.75**	**0.002**	ctr v. sal x year	3.58	1.09	3.28
f: offspring survival:								
intercept	1	30.6	1.16	0.29		-2.01	2.08	-0.97
treatment	2	48.9	0.02	0.98	BA v. sal	0.15	0.70	0.21
					BA v. ctr	0.07	0.88	0.08
year	1	73.0	0.13	0.72	2011 v. 2012	-0.31	1.14	-0.28
habitat	1	29.9	0.04	0.85	man v. unman	-0.11	0.58	-0.20
female phenotype	2	28.1	0.04	0.96	philop v. unkn	0.10	0.73	0.13
					philop v. imm	-0.11	0.73	-0.14
number of siblings	1	32.4	0.31	0.58		0.16	0.30	0.56
timing injection	1	30.6	0.16	0.70		0.02	0.04	0.40
treatment x year	1	73.0	0.00	0.99	ctr v. sal x year	-0.03	1.87	-0.02
g: female survival:								
intercept	1	72.7	0.32	0.58		-4.21	8.73	-0.48
treatment	2	84.8	0.59	0.56	BA v. sal	1.13	2.63	0.43
					BA v. ctr	-1.00	2.23	-0.45
year	1	45.2	0.69	0.41	2011 v. 2012	-2.10	3.82	-0.55
habitat	1	43.7	0.99	0.33	man v. unman	1.76	1.77	0.99
female phenotype	2	38.3	0.34	0.71	philop v. unkn	-1.82	2.49	-0.73
					philop v. imm	-2.40	2.99	-0.80
female age	1	30.7	1.94	0.17		-0.40	0.29	-1.39
number of fledglings	1	80.7	1.24	0.27		0.80	0.71	1.11
timing injection	1	41.4	0.99	0.33		0.19	0.19	0.99
treatment x year	2	96.0	0.04	0.96	BA v. ctr x year	-0.44	4.36	-0.10
					BA v. sal x year	7.40	28.83	0.26

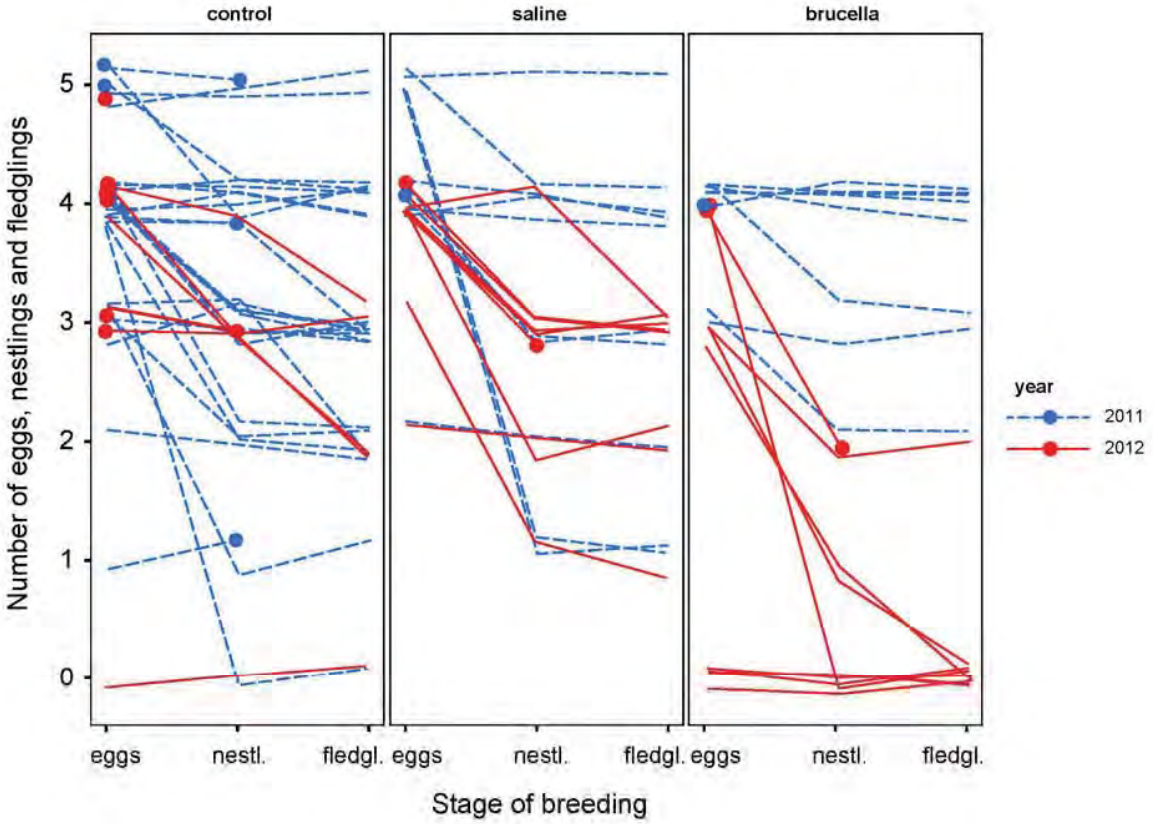

Figure 4. Change in reproductive allocation (number of eggs, nestlings, fledglings) in the three treatment groups (*Brucella abortus*: dotted lines, saline: dashed lines, control: solid lines), split by year (2011: favorable year, 2012: unfavorable year). In nests which failed due to predation, the last measurement is marked with a circle. The nesting success was much higher in 2011 than in 2012, and treatment groups showed no difference in reproductive allocation. In 2012 *Brucella abortus* injected females had a much lower allocation (five females did not initiate a nest; three females abandoned the nest). One control female did not imitate a nest in 2012 since her male died before egg laying. For clarity the values are jittered around the exact numbers on the Y-axis to make overlapping lines visible.

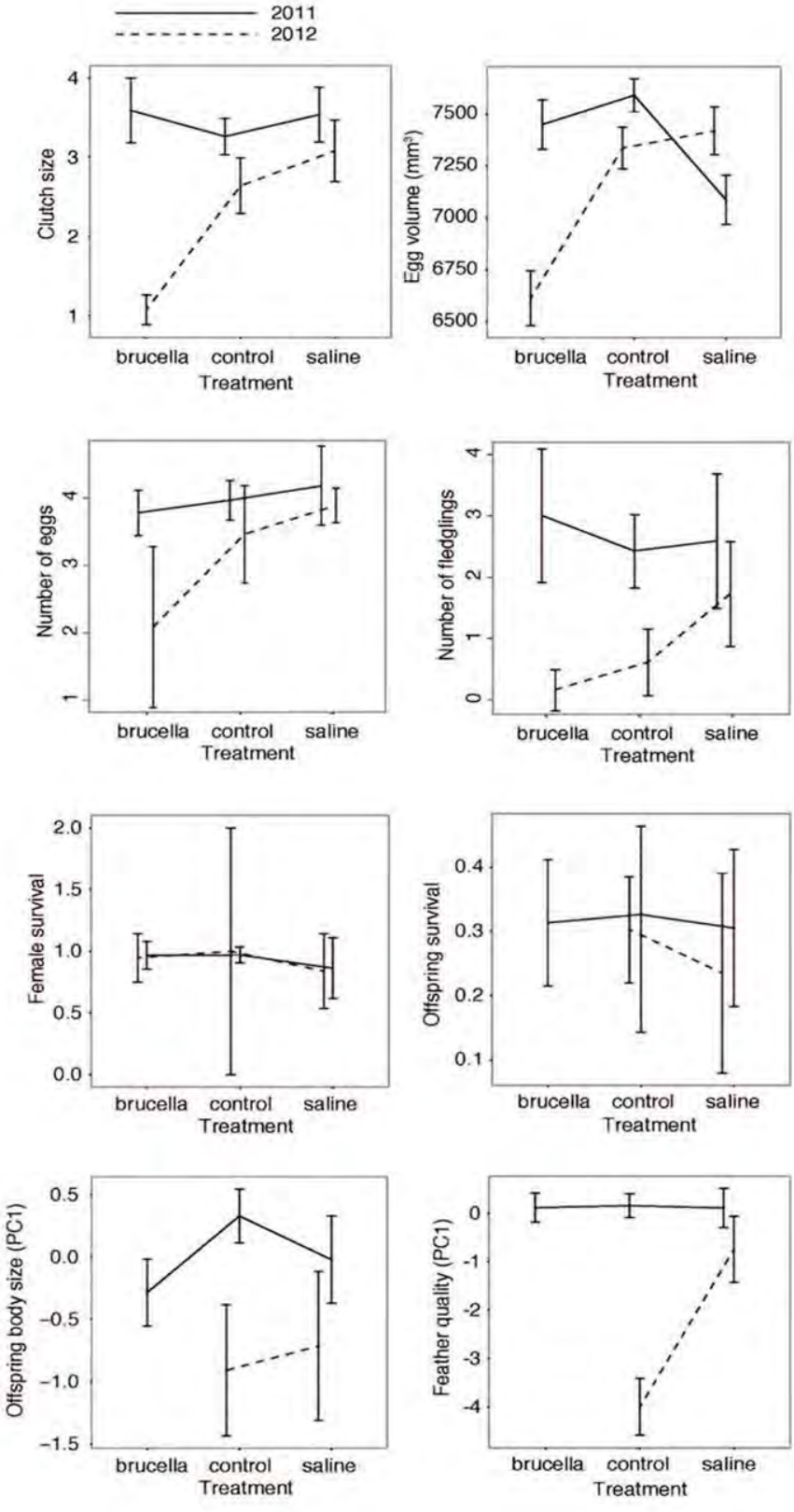

Figure 5. Influence of *Brucella abortus* injection 2-4 weeks before egg laying on the number of eggs laid, egg volumes, offspring feather quality, offspring adult body size, as well as offspring and female survival until next year in the three treatment groups. BA injections only influenced egg volumes, reproductive allocation and offspring feather quality in 2012. No measures for offspring of BA treated females were available in 2012 since most BA injected females elected to skip breeding or abandoned their clutch soon after egg laying. No long-term effects on either offspring or the females were found. Detailed statistics are given in Table 2.

4.5 Discussion

Our results show that reproductive allocation in the Siberian jay, a long-lived bird species, depends on both annual conditions and female body condition. Long-term data revealed that females reduce the number of eggs in bad years with a high risk of reproductive failure (Fig. 1), but rarely refrain from breeding. Accordingly, females produce fewer fledglings in bad years, but neither the annual conditions nor the number of fledglings affect female survival, first-year offspring survival or offspring body size (Table 1). Thus, the number of eggs and female survival both had a lower variance than the number of fledglings, reflecting that a substantial proportion of nests failed (Fig. 3). An experimental challenge with a novel pathogen replicated these patterns. Females with an experimentally reduced body condition elected to skip breeding only in a bad year, but we did not detect any down-stream effects. Thus, condition-dependent reproductive allocation acts to keep costs of reproduction in a long-lived species constant, casting new light on the evolution of reproductive trade-offs in birds.

In a number of species individuals reduce their reproductive investment (even to the point of refraining from breeding altogether) under harsh environmental conditions (Grant et al. 2000, Cubaynes et al. 2011, Pardo et al. 2014) and/or when in low body condition (Clutton-Brock 1991, Roff 1993, Erikstad et al. 1998). Our experimental challenge with BA demonstrated that the joint occurrence of harsh environmental conditions and reduced body condition lead to a reduced reproductive allocation, but not to any detectable down-stream effect (Fig. 2, 4-5, Table 2). Thus, this is the first experimental study confirming that long-lived species indeed reduce their reproductive allocation under harsh environmental or low body conditions, even leading to intermittent breeding (Shaw and Levin 2013). In contrast to nests of untreated females that usually fail late in the nestling stage due to predation, most BA injected females that laid eggs abandoned them early on in incubation or soon after hatching (Fig. 4). Thus, BA injected females seemed to reduce downstream costs to themselves by abandoning their nests early on, suggesting that they assessed costs of reproduction continuously.

Given the widespread occurrence of intermittent breeding in long-lived bird species (Bradley et al. 2000, Covas et al. 2004, Shaw and Levin 2013), brood and clutch size manipulations provide limited insights into the consequences of reproductive decisions. Moreover, empirical studies rarely assess offspring quality or follow post-fledging survival (Santos and Nakagawa 2012) and exclude females that exhibit intermittent breeding. Models have focused so far on the trade-off between parental survival and reproductive allocation (Hamel et al. 2010), ignoring intergenerational trade-offs. Nevertheless, offspring quality is a vital contributor to fitness given that offspring need to survive and successfully reproduce (Williams 1994). Our longitudinal and experimental data both suggest that females regulate the cost of reproduction (assessed as survival cost for females and offspring, and offspring quality) largely by adjusting the initial reproductive investment (i.e., the number of eggs laid).

Previous studies that experimentally increased costs of reproduction have reported downstream fitness consequences for females (Ardia et al. 2003) or offspring (De Kogel 1997, Krist 2011, Santos and Nakagawa 2012). Small egg size and/or poor early condition has negative fitness consequences for offspring in many species (Metcalfe and Monaghan 2001, Cam and Aubry 2011, but see Drummond et al. 2011). However, most experimental studies on reproductive allocation trade-offs in birds have particularly investigated short-lived species breeding in nest boxes (Santos and Nakagawa 2012), and manipulated birds after egg laying. Given these biases, it remains unclear whether long-lived bird species in general adjust their initial reproductive investment to produce offspring of even quality under varying environmental and body conditions, without paying a survival cost.

Studies often measure reproductive allocation at different reproductive stages (clutch or litter size vs. number of fledglings or weaned offspring), but the losses that occur between the stages differ greatly across species and across taxonomical classes. In many egg-laying species, nest predation is rampant, and thus, the difference between the number of eggs and the number of fledglings can be large, as is the case in Siberian jays. Similarly, predation and starvation of young mammals can largely increase the number of born and weaned young. Moreover, variation in individual quality (van Noordwijk and de Jong 1986, Stearns 1992) will further increase the variance of

reproductive output and/or female survival. Thus, it is important to assess the changes in reproductive allocation between different stages and to specify the processes leading to a high variance of offspring quantity, facilitating future comparative work focusing on measures of reproductive allocation.

Although long-lived mammals (Hamel et al. 2010) and Siberian jays both have a high variance in initial reproductive allocation but a low variance in female survival, the underlying processes are likely to differ across taxonomical classes. Long-lived mammals (i.e., species with a maximum lifespan above the mean: 16.3 years; (Jones et al. 2009)) require 3.6 times longer than long-lived birds (i.e., species with a maximum lifespan above the mean: 15.7 years; (Valcu et al. 2014)) to raise their offspring to independence (431 vs.120 days; Jones et al. 2009, Drobniak et al. 2015), affecting the evolution of reproductive allocation strategies. At intermediate to high latitude, females of long-lived mammals are pregnant during winter with limited resources available, and in several long-lived mammal species, offspring experience high variance in first-year mortality (Pereira and Fairbanks 1993, Hastings et al. 1999, Gaillard et al. 2000). In contrast, birds mostly breed during the time of the year when the most resources are available, and are in a better position to match their reproductive allocation to the conditions during the breeding season. Thus, it would be crucial to know at which stage variance in reproductive output arises to understand the selective pressures that influence the evolution of reproductive allocation across taxonomical classes.

To conclude, our study shows that females in a long-lived bird species exhibit intermittent breeding when experiencing both harsh environmental conditions and experimentally reduced body condition. Yet, when females did commit to breeding, offspring quality (i.e., body size) did not vary between years or individuals, nor did it influence the survival of females or fledged offspring. Offspring quality has been shown to have downstream fitness effects (Lock 2012, Burton and Metcalfe 2014), highlighting that future life-history models on reproductive allocation should consider the variance of reproductive allocation (i.e., number of eggs or litter size), reproductive output (i.e., number of fledglings or weaned offspring), and offspring quality and survival. Future long-term studies will help to determine whether other long-lived bird species also produce high

–quality offspring independent of environmental or female body condition, and display a low variance of initial reproductive allocation as well as female and offspring survival.

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4.6 Supplementary Material

Supplementary methods: Simulation to test for a link between average clutch size and the proportion of successfully breeding females.

We performed a simple simulation to test whether a larger average clutch size influenced the proportion of successfully breeding females, using the basic life-history parameters from our study population. These two quantities could be correlated if nests with a small clutch size are more likely to fail than nests with a larger clutch size. Given that females do not initiate a clutch only in exceptional cases, we excluded these cases. We simulated a multi-seasonal breeding of a theoretical population of females to confirm that any relationship between clutch size and the mean breeding success in the study population is not a mathematical artefact. We modelled 500 times a hypothetical population of n=50 females in each breeding season. Females have an annual mortality rate sampled from a uniform distribution between 5 and 15% (Ekman and Griesser 2016), and every deceased female is replaced by a new female (Ekman et al. 2001). Within each breeding season, random females breed successfully with the probability of p = 42% (Griesser et al. 2014). Clutch sizes are sampled from a zero-truncated Poisson distribution with mean λ = 3 (Eggers et al. 2005a). Within each of the 500 iterations we determined the slope of the regression between the within-season average clutch size and mean annual nesting success (b). Our simulation indicates that the relationship shown in Figure S1 could not arise due to a correlation between average clutch size and the proportion of successfully breeding females. Thus, our null

hypothesis is valid, and the demonstrated relationship between initial reproductive allocation and mean annual breeding success represents a true biological phenomenon.

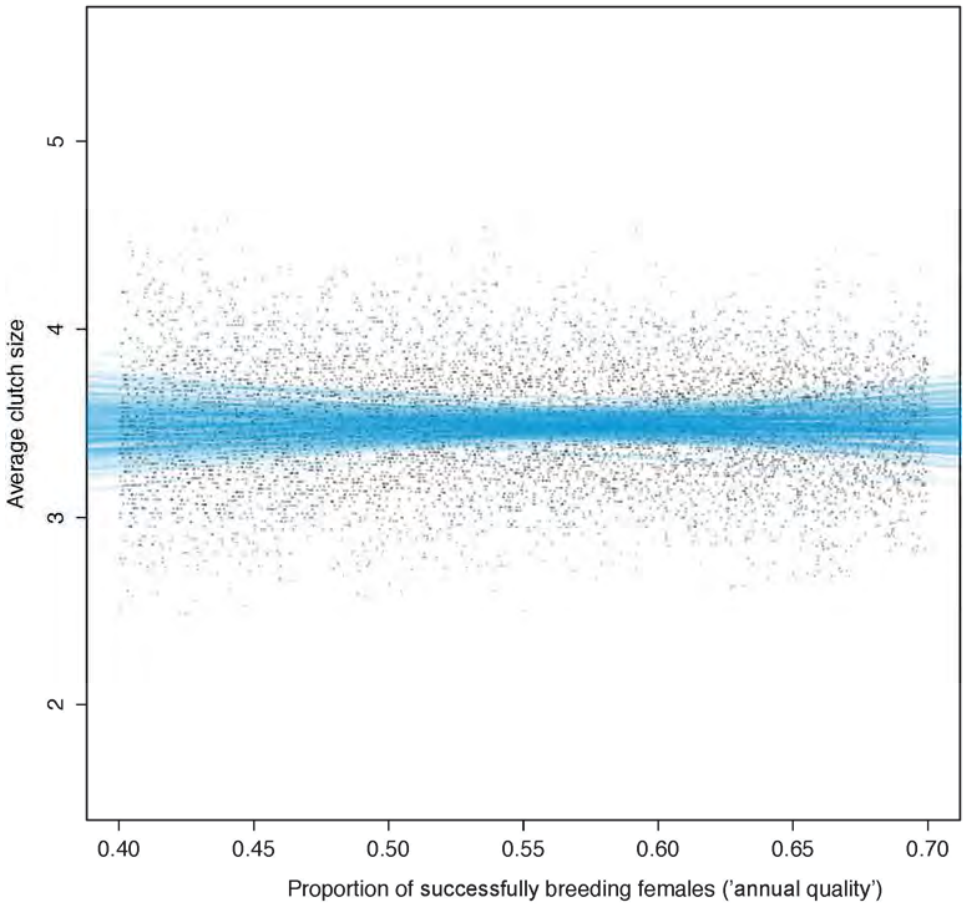

Figure S1: Outcome of the simulation to test for the link between average clutch size and the proportion of successfully breeding females.

Supplementary tables

Table S1. Overview of the number of Siberian jay females involved in experimental treatments. Females were injected ahead of egg-laying with *Brucella abortus* (BA), saline solution, or remained untreated (control). Territories where we were unable to find the nest due to radio-tag failure or predation of a breeder are not shown.

Year	2011 (favourable year)			2012 (unfavorable year)		
treatment	philopatric females	immigrant females	unknown status	philopatric females	immigrant females	unknown status
BA	2	6	1	3	7	2
saline	3	6	2	2	7	0
control	5	6	19	2	0	11

Table S2. Principal Component analyses of offspring body size (a) and feather quality (b).

(a)

Component	Wing length loading	Tarsus length loading	Eigenvalue	Proportion variance explained
PC1	0.88	0.88	1.54	0.77
PC2	-0.48	0.48	0.46	0.23

(b)

Component	Fault bars wing loading	Fault bar tail loading	Eigenvalue	Proportion variance explained
PC1	0.84	0.84	1.41	0.71
PC2	-0.54	0.54	0.59	0.29

Table S3: Generalized linear mixed models assessing the influence of experimental treatment in the first year on the reproductive investment and female survival in the second year (*n*=15 females that were injected repeatedly). Significant factors highlighted in bold. den. *df*: denominator degree of freedom; *F*: conditional *F*-statistic.

Model	Factor	*df*	den. *df*	*F*	*p*
Number of eggs	**intercept**	**1**	**61**	**37.86**	**0.00001**
	effect of previous experiment	3	61	1.33	0.27
	habitat (natural vs. managed)	1	61	0.01	0.92
	female phenotype	2	61	0.92	0.40
	female age	1	61	1.72	0.19
Number of fledglings	**intercept**	**1**	**55**	**23.84**	**0.00001**
	effect of previous experiment	3	55	1.84	0.15
	habitat (natural vs. managed)	1	55	0.08	0.78
	female phenotype	2	55	0.80	0.46
	female age	1	55	3.57	0.06
Female survival	**intercept**	**1**	**31.9**	**6.58**	**0.02**
	effect of previous experiment	3	56	0.21	0.89
	habitat (natural vs. managed)	1	33.4	0.57	0.46
	female phenotype	2	50.7	0.44	0.64
	female age	1	29.8	1.28	0.27

Chapter 5

Experimentally increased costs of parental care are shunted to offspring in species with extended care

Gretchen F. Wagner [1], Emeline Mourocq[1], Michael Griesser[1]

[1] Department of Anthropology, University of Zürich, Zürich, Switzerland

5.1 Abstract

Biparental care systems are a valuable model to examine conflict and cooperation between unrelated individuals, as the reproductive decisions of each parent determine their own fitness. A common experimental technique for testing responses to changes in the costs of parental care is to temporarily handicap one parent, inducing a higher cost of providing care. However, dissimilarity in experimental designs of these studies has hindered interspecific comparisons of the patterns of cost distribution between parents and offspring. Here we apply a comparative experimental approach by handicapping parents of five bird species using the same experimental treatment. In some species, a decrease in care by a handicapped parent was compensated by its partner, while in others the increased costs of care were shunted to the offspring. Parental responses to an increased cost of care primarily depended on the total duration of care that offspring require. However, life history pace (i.e., adult survival and fecundity) did not influence parental decisions when faced with a higher cost of caring. Our study highlights that a greater attention to intergenerational trade-offs is warranted, particularly in species with a large burden of parental care. Moreover, we demonstrate that parental care decisions may be weighed more against physiological workload constraints than against future prospects of reproduction, supporting evidence that avian species may devote comparable amounts of energy into survival, regardless of life history strategy.

5.2 Introduction

Parental care is widespread in animals, but its expression varies greatly among and within species (Cockburn 2006, Royle et al. 2012) as well as within individuals (Eggers et al. 2008, Ghalambor et al. 2013, Caro et al. 2016). Biparental care is a particularly interesting system of parental care, as the product of the interactions between the parents is vital to the fitness of both individuals. Birds are unique among the taxonomic classes in regard to the prevalence of biparental care: both parents contribute care to the offspring in an estimated 90% of bird species (Cockburn 2006), while in other clades biparental care is much rarer (percentage of genera with bi-parental care: teleost fish: 3%, anurans: 1%, mammals: 9%, squamate reptiles: 0%, Gross and Sargent 1985; insects: 22% of species with any parental care, Suzuki 2013).

Biparental care relies on cooperation between parents to ensure the survival of their offspring, but is also a source of conflict. Both parents face a trade-off between current and future reproduction and should strive to reduce their own effort, in balance with their partner's effort, to ensure that offspring receive enough total care to survive while lessening current costs of parental care for themselves (Trivers 1972, Drent and Daan 1980). A pioneering model suggested that investment in parental care of both parents can be an evolutionary stable strategy (ESS) if one parent reduces its effort, its partner partially compensates and the increased costs are distributed between the partner and the offspring (Houston and Davies 1985). Recent models have predicted that negotiation between the parents could lead to partial, full or no compensation by partners, depending on the costs and benefits associated with care (Jones et al. 2002, Johnstone and Hinde 2006). This negotiation process has been suggested to be influenced by several species traits, such as brood size, developmental mode and lifespan (Silver et al. 1985, Kokko and Jennions 2003, Olson et al. 2008), however experimental tests of these ideas are lacking.

A common experimental technique for testing changes in the costs of parental care is to temporarily handicap one parent, thereby increasing the cost of providing care. In birds, this is often accomplished through the removal of flight feathers. These handicapping experiments have demonstrated large between-species variation in responses to changes in one parent's physical condition, across both parents and their offspring (Table 1). Handicapped birds may maintain or

Table 1. Results from previous studies that increased the costs of parental care through feather removal.

Species	Condition			Care Behavior		Reference
	Focal	Partner	Offspring	Focal	Partner	
blue tit *Cyanistes caeruleus*	-	-	≈	-	≈	(Slagsvold and Lifjeld 1990)
coal tit *Parus ater*	-					(Slagsvold and Lifjeld 1990)
great tit *Parus major*	-	≈	-			(Slagsvold and Lifjeld 1990)
tree swallow *Tuchycineta bicolor*			≈	≈	+	(Whittingham et al. 1994)
Leach's storm-petrel *Oceanodroma leucorhoa*	≈		-	-		(Mauck and Grubb Jr 1995)
thin-billed prion *Pachyptila belcheri*	-		≈			(Weimerskirch et al. 1995)
tree swallow *Tuchycineta bicolor*	-			-		(Winkler and Allen 1995)
pied flycatcher *Ficedula hypoleuca*	≈	≈	-	≈	≈	(Moreno et al. 1999)
great tit *Parus major*	≈	≈	≈	-	+	(Sanz et al. 2000)
blue-footed boobie *Sula nebouxii*	-		-			(Velando 2002)
blue-footed boobie *Sula nebouxii*	≈	-	-			(Velando and Alonso-Alvarez 2003)
common tern *Sterna hirundo*	-		+			(Nisbet et al. 2004)
Cory's shearwater *Calonectris diomedea*	≈		-	-		(Navarro and González-Solís 2007)
cape gannet *Morus capensis*	-	≈	-	-	+	(Bijleveld and Mullers 2009)
little auk *Alle alle*	-	-	-			(Harding et al. 2009)
black-legged kittiwake *Rissa tridactyla*	-	≈	≈	≈	-	(Leclaire et al. 2011)
thick-billed murre *Uria lomvia*	≈		-			(Jacobs et al. 2013)
great tit *Parus major*	-		-	-		(Wegmann et al. 2015)

reduce their physical condition and/or their parental effort. Non-experimental individuals may fully compensate their partner's decrease in care, partially compensate, or copy the behavior of their partner (i.e., decrease care if their partner decreases care). Similarly, the condition of offspring may improve, decline, or stay constant. Although there have been many experimental manipulations of parental care, to our knowledge only one meta-analysis has previously examined

the responses comparatively (Harrison et al. 2009). However, due to variation in the types of manipulation (e.g. clipping feathers vs. adding weight), the behavior examined (e.g., feeding vs. incubation) and the types of responses recorded (e.g., parental behavior vs. parental condition), a thorough examination of the mitigating factors for patterns of parental care across species has not been possible. Indeed, this meta-analysis showed that the type of manipulation played a key role in explaining heterogeneity in parental responses to manipulation of care and that responses differed depending on the behavior being focused on, while species traits that may have accounted for interspecific differences were largely excluded from the analyses.

A drawback of many handicapping studies is that they measure effects on a single trait or individual, by focusing only on the condition or behavioral changes of the handicapped parent, its partner or their offspring (see Table 1). Consequently, it is difficult to determine how experimental effects are distributed between parents and offspring in many cases. Furthermore, the most common measure taken has been changes in the condition of the handicapped individual (Table 1), usually in terms of body mass, which are frequently attributed to an increased reproductive effort. However, these responses may reflect functional corrections to wing loading rather than adverse effects of handicapping (Norberg 1981, Lind and Jakobsson 2001), confounding whether there are any changes in reproductive effort. Because changes in the body mass of handicapped birds are difficult to interpret, it is important to measure parental effort directly, via behavioral responses, in combination with the condition of the offspring, so that relative effects can be properly estimated across all of the family members.

Here we handicapped parents in five bird species with bi-parental care, resulting in one partner facing higher costs of offspring provisioning, which must be paid by the treated bird, its partner, or their offspring. We analyzed the results comparatively to examine differences in parental care behavior of each parent and any effects on nestling condition. Life-history theory predicts that long-lived species should prioritize survival (and thus future reproduction) over current reproduction, and they are consequently expected to be less willing to increase their parental effort compared to short-lived species (Williams 1966, Drent and Daan 1980). However, a more recent comparative analysis on costs of care suggests that all individuals may allocate the same

amount of energy to survival, regardless of their life-history pace (Santos and Nakagawa 2012). Thus, we expected that responses will vary across a life-history spectrum, but that life history pace alone will not account for interspecific differences.

5.3 Methods

Study species

We handicapped individuals of five bird species with biparental care in southern Spain during the breeding seasons of 2013 and 2014. The experiment was conducted in populations of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and woodchat shrikes (*Lanius senator*) in the Cordoba region (37°95'N, 4°40'W), and black wheatears (*Oenanthe leucura*) and European bee-eaters (*Merops apiaster*) in the Guadix region (37°25'N, 3°05'W). All nests used in the analyses had two adults, presumably the mother and father, attending to the nestlings. At least one parent was marked for individual identification prior to the experiment, with a combination of plastic colored rings or a temporary mark on their feathers. Because European bee-eaters sometimes have helpers at the nest, both parents were marked early in the nest stages (building or incubating) to reduce the chances of marking a non-breeder, and each nest included in this study was checked for the presence of only 2 adults attending the nest at the time of the experiment.

Experimental Design

Experiments were started at each nest based on the developmental stage of the nestlings (as feather growth begins), rather than absolute age, to allow for a better comparison between species with different development schedules. The experimental procedure spanned five days. Each nest was recorded with a video camera to obtain the feeding rate for 2-4 hours on the first, second, fourth and fifth days of the experiment. The duration of recording was determined prior to the experiment through observations of each species, and was based on the natural feeding rate to conservatively ensure a minimum of ten feeding visits per observational bout. Recordings were made at the same time for each nest, and nests were assigned to morning, midday or afternoon recordings using a balanced random design.

On the third day of the experiment one of the adults at each nest was caught and either handicapped, by removing the 7th and 9th primary feathers on each wing, or was handled (with simulated feather removal) and released as a control. Removal of flight feathers has been demonstrated to increase the energetic demands of flight by increasing wing loading (Pennycuick 1989, Hedenström and Sunada 1999), thus increasing the cost of parental care during foraging for provisioning.

After recording on the first day, all nestlings were marked for individual identification with a non-toxic permanent marker on one leg. Each nestling was weighed with a digital scale and its wing and tarsus length were measured with dial calipers (0.1mm accuracy) on the first, third and fifth day of the experiment. All nestling measurements within a nest were taken by the same experimenter to maintain consistency across days.

Statistical Analyses

We predicted that the visitation rates of parents after one parent is handicapped may be influenced by the adult survival rate, body mass, the body mass–scaled initial reproductive allocation (total mass of eggs produced annually divided by adult body mass, following Sibly et al. 2012), the duration that offspring require provisioning, and the duration that offspring stay with their parents subsequent to nutritional independence. We used a principal component analysis (PCA) to reduce the dimensionality of these predictors, as most of them exhibited moderate to strong correlations (Table S1). Because the units of measurement for traits differed, we relied on the correlation matrix among variables to generate PCA scores rather than the covariance matrix (Graham 2003). Both the inspection of a Scree plot and Eigenvalues suggested the extraction of 2 principal components (PCs). To simplify the factor structure by maximizing the variances of loadings and hence facilitate their interpretation, we first performed an oblique (oblimin) rotation of the components, which indicated that the resulting factors were not substantially correlated ($r=0.21$). We then applied a varimax rotation to the original components. Differences in results of the rotation techniques were negligible, and did not affect the overall pattern of loadings, so we retained the varimax rotation in further analyses (Kieffer 1998).

The principal components analysis resulted in the extraction of two PC variables (Table S1) which cumulatively explained 79% of the variance. The first component, hereafter labelled “duration of care”, included the number of days that offspring are provisioned by their parents (‘care time’), body mass, and the number of days that offspring stay with their parents post-nutritional independence ('family time', Drobniak et al. 2015). A high value of this component signifies species with long periods of parental care. The second component, hereafter labelled “life history pace”, included adult survival rate and the index of reproductive allocation (see above). A high value of this component signifies parents with long expected lifespans and low annual reproductive investment.

We fit linear mixed models using a Bayesian framework with Markov chain Monte Carlo (MCMC) methods with the package MCMCglmm (Hadfield 2010) in R 3.1.0 (R Core Team 2014) to examine among-species responses to the handicapping procedure. All models were run for 100’000 iterations, with a burn-in phase of 2’000 iterations and a thinning interval of 100, which resulted in approximately 1’000 samples from the posterior distributions for each model parameter. A reasonably normal distribution of residuals was confirmed for all models. Model convergence was confirmed by visual examination of trace plots and calculation of autocorrelation between iterations. Because initial models included several 2- and 3-way interactions (see below), non-significant interactions ($p>0.05$) were removed from initial models using a backwards elimination procedure, except for the interaction between treatment and phase. The interaction between treatment and phase was expected a priori and is the main result of our experiment, as we only expect an experimental effect during the post-treatment phase. Results of all initial models, prior to removal of any non-significant terms, are included in the Supplementary Material, to facilitate comparison of models and effect sizes for both significant and non-significant factors.

Visitation rates

Visitation rates were measured as the number of nest visits per hour per nestling. Although we did not confirm that every visit involved food delivery, visitation during the nestling phase is a common proxy for offspring provisioning (Mariette et al. 2011, Mutzel et al. 2013). These rates were averaged for experimental days 1 and 2, i.e, ‘pre-treatment’ phase, and experimental days 4

and 5, i.e., 'post-treatment' phase. We first analyzed sources of variation in visitation rates among the tested species using linear mixed-effect models with the total feeding rate at the nest as the response variable. Brood size, duration of care, life history pace, phase, and treatment were included as fixed effects, with random intercepts for species and nest identity. Because of the experimental design, changes in chick provisioning after the treatment could potentially be confounded by an effect of time, if feeding rates naturally change over the nesting period. Therefore, treatment effects were also examined by including three-way interactions, and their contained two-way interactions, of phase and treatment with each principal component. Non-significant main effects were retained in the final model while non-significant interactions were removed from final models, except for the interaction between treatment and phase.

Our analyses revealed a significant 3-way interaction between phase, treatment and duration of care for the total visitation rate (see Results). To interpret this interaction, we carried out two additional models, examining treatment effects in the pre-treatment phase and the post-treatment phase separately. These models included brood size, duration of care, life history pace, and the two-way interaction between duration of care and treatment as fixed effects, with species as a random factor.

We then examined treatment effects on the feeding rates of the focal individuals (i.e. handicapped or control-caught). We included brood size and separate three-way interactions between treatment, phase, and each principal component (and their contained two-way interactions and main effects) as fixed effects, with species and nest identity as random factors. Non-significant interactions were sequentially removed from final models, but non-significant main effects were retained. Because we found no significant 3-way interactions in this model, no additional models were run.

Nestling Growth

We analyzed sources of variation in nestling growth among all of the tested species using separate linear mixed-effect models of nestling changes in mass, tarsus length, and wing length. Each response variable was measured as the difference in each parameter between the pre-treatment

phase (days 1-2), and the difference in each measurement of the post-treatment phase (days 4-5). Brood size, duration of care, life history pace, phase, and treatment were included as fixed effects. Random intercepts were specified for species, nest identity, nestling identity (unique combinations of nest identity and nestling number), and nest phase (unique combinations of nest identity and phase). Changes in chick growth after the treatment could potentially be confounded by an effect of time, if growth rates naturally change over the nesting period. Therefore, treatment effects were examined by including three-way interactions, and their contained two-way interactions, of phase, treatment and each principal component. Because a significant interaction between phase and treatment was expected a priori, this interaction was maintained in all models regardless of significance. All other non-significant interactions were removed from final models, but non-significant main effects were retained.

Our analyses revealed a significant 3-way interaction between phase, treatment and duration of care for changes in nestling body mass (see Results). To interpret this interaction, we carried out 2 additional models, examining the treatment effects of nestling mass change separately in the pre-treatment phase and the post-treatment phase. These models included brood size, adult survival rate, and the two-way interaction between duration of care and treatment as fixed effects, with species as a random factor.

5.4 Results

Visitation rates

Results of visitation rates (visits per hour and nestling) are based on 72 nests (Table 2). Independent of the treatment, a long duration of care was related to higher individual parental visitation rates (Table 3) and marginally related to higher total visitation rates (Table 4). Neither the brood size nor life history pace were related to individual (Table 3) or total (Table 4) visitation rates. The visitation rate of focal individuals did not change between experimental phases in control nests, while focal parents reduced their visits after being handicapped (Table 3, Fig. 1). Although the individual rates were significantly lower in the handicapped group, this effect did not interact with any other explanatory variables.

Table 2. Sample sizes of nests and nestlings for each species.

common name	scientific name	treatment n		control n	
		nests	nestlings	nests	nestlings
Blue tit	*Cyanistes caeruleus*	6	44	7	52
Black wheatear	*Oenanthe leucura*	8	28	7	25
European bee-eater	*Merops apiaster*	8	39	7	28
Great tit	*Parus major*	7	52	7	51
Woodchat shrike	*Lanius senator*	7	26	8	38

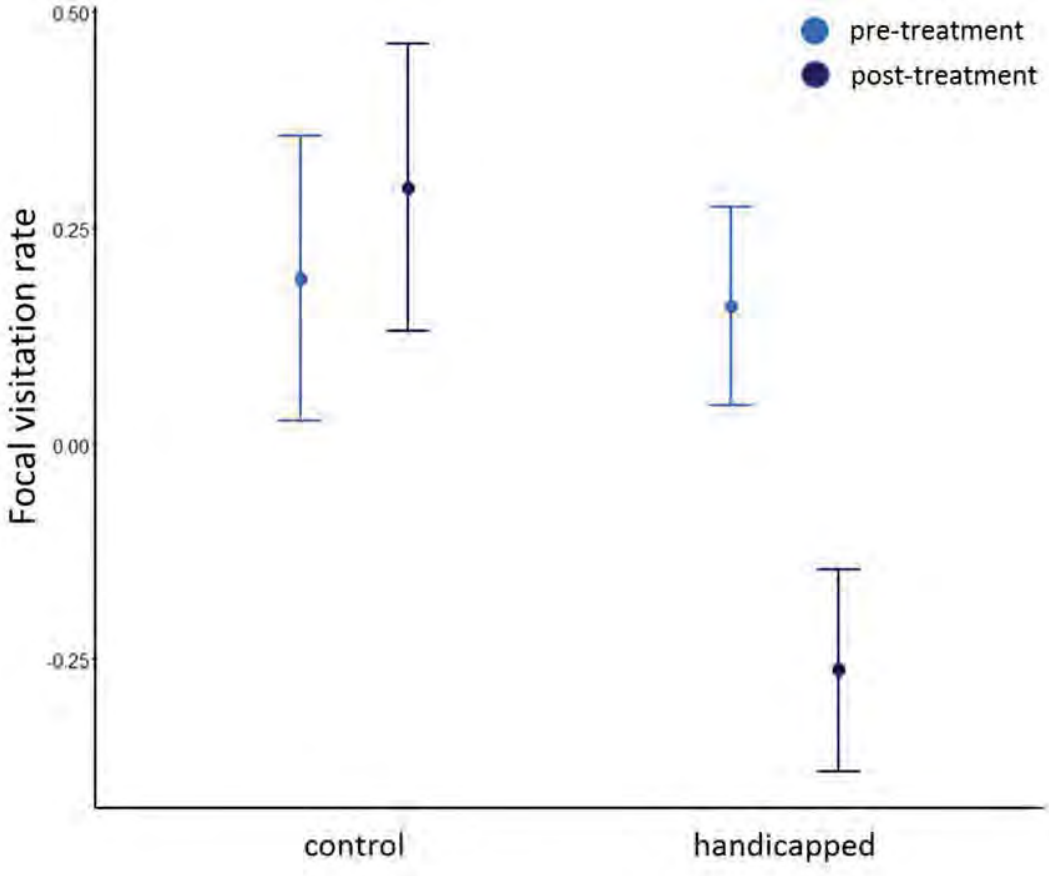

Figure 1. Standardized predicted values (+/- SE) from mixed model of focal bird per-nestling visitation rates. Prior to the treatment, visitation rates did not differ between the control group and treatment group. After the treatment, handicapped birds reduced their visitation rate.

Table 3. Selected mixed model results of effects on focal individual visitation rate. Significant effects (p<0.05) are denoted in bold. Full model results are presented in Table S2.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.350	-0.310	0.842	0.151
duration of care	**1.059**	**0.509**	**1.560**	**0.016**
life history pace	0.341	-0.092	0.829	0.120
brood size	0.266	-0.224	0.693	0.325
pre-treatment phase	-0.140	-0.539	0.230	0.471
treatment	**-0.619**	**-1.021**	**-0.245**	**<0.001**
treatment x pre-treatment phase	**0.535**	**0.032**	**1.072**	**0.047**
random effects				
species	0.295	<0.001	1.361	
nest	0.006	<0.001	0.051	

Total visitation rates were significantly affected by a 3-way interaction between treatment, phase and duration of care (Table 4). Post-hoc examination of this relationship revealed that there was no difference between the pre-treatment phase of the control and the handicapped groups in total visitation rate (estimate= -0.13 95%CI= -0.40, 0.16, p=0.36; Fig. 2A), nor any effects of any of the explanatory variables (Table A4). In contrast, the total visitation rates in the post-treatment phase were lower in handicapped individuals than control individuals (estimate= -0.46, 95%CI=-0.81,-0.12, p=0.008, Table S5). Duration of care interacted with the treatment, indicating that the experimental effect was strongest in species with long parental care periods (estimate= -0.35, 95%CI=-0.70, -0.03; p=0.040; Fig. 2B).

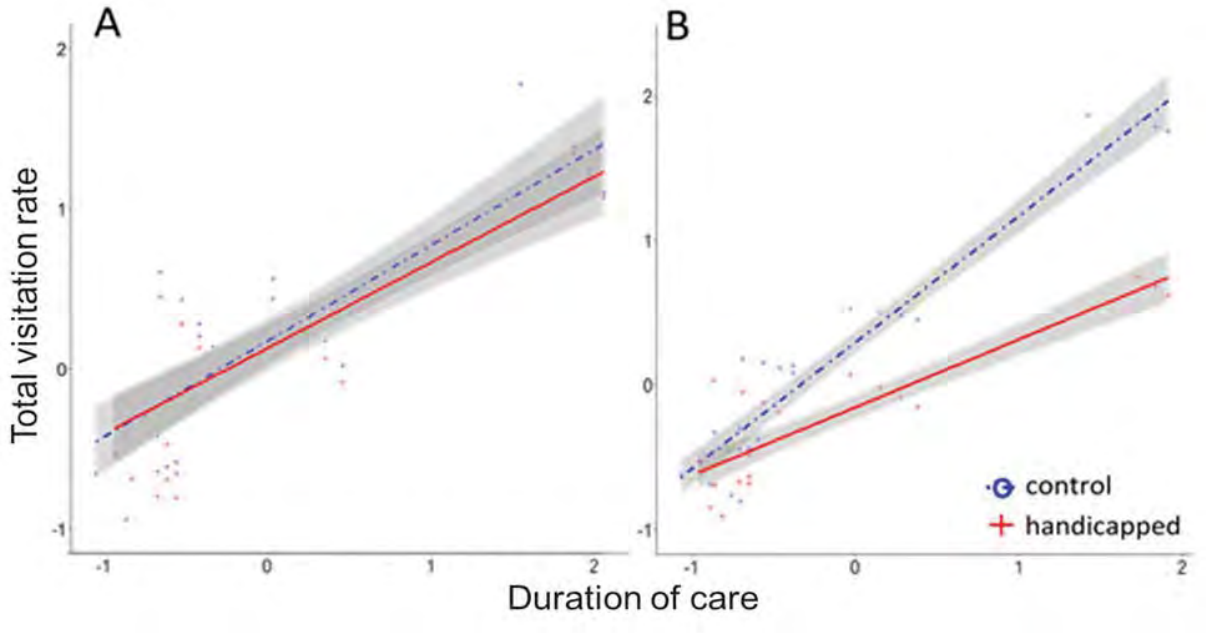

Figure 2. Standardized model-predicted total visitation rates varied according to duration of care. (A) Handicapped and control groups had similar visitation rates during the pre-treatment phase (B) Total visitation rates were lower in the handicapped group during the post-treatment phase, particularly for species with long durations of care. Shaded area represents 95% confidence interval.

Table 4. Selected mixed model results of effects on total visitation rate at the nest. Significant effects ($p<0.05$) are denoted in bold. Full model results are presented in Table S3.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.217	-0.540	0.887	0.443
duration of care	0.699	-0.129	1.411	0.065
life history pace	0.315	-0.096	0.737	0.120
brood size	-0.094	-0.326	0.168	0.444
pre-treatment phase	-0.100	-0.319	0.075	0.310
treatment	**-0.424**	**-0.711**	**-0.162**	**0.006**
treatment x pre-treatment phase	**0.312**	**0.055**	**0.564**	**0.016**
duration of care x pre-treatment phase	0.076	-0.163	0.294	0.495
duration of care x treatment	-0.287	-0.601	0.006	0.053
duration of care x pre-treatment phase x treatment	**0.334**	**0.050**	**0.613**	**0.020**
random effects				
species	0.785	<0.001	2.642	
nest	0.186	0.087	0.291	

Nestling Growth

Nestling growth data was based on 384 nestlings (Table 2). Changes in nestling mass (Table 5) mirrored the results of total visitation rates and was influenced by a 3-way interaction between duration of care, phase, and treatment. The change in nestling mass did not differ in the pre-treatment phase according to any of our explanatory variables (Fig. 3A, Table S7). In the post-treatment phase (Table S8), the change in body mass of nestlings in the handicapped group decreased with an increasing duration of care, while the mass change of nestlings in the control group increased with an increasing duration of care (Fig. 3B). Changes in nestling mass also depended on life history pace, independent of the treatment, but was not related to any other explanatory variable.

Table 5. Selected mixed model results of changes in nestling mass. Significant effects (p<0.05) are denoted in bold. Full model results are presented in Table S6.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.167	-0.120	0.460	0.233
duration of care	0.050	-0.218	0.315	0.724
life history pace	**0.227**	**0.035**	**0.412**	**0.036**
brood size	0.030	-0.181	0.222	0.779
pre-treatment phase	-0.175	-0.433	0.099	0.234
treatment	-0.309	-0.682	0.075	0.108
treatment x pre-treatment phase	0.309	-0.073	0.680	0.122
duration of care x pre-treatment phase	0.138	-0.135	0.412	0.330
duration of care x treatment	-0.345	-0.688	0.019	0.057
duration of care x pre-treatment phase x treatment	**0.429**	**0.017**	**0.776**	**0.026**
random effects				
species	0.003	<0.001	0.010	
nest	0.281	0.132	0.474	
nestling	0.001	<0.001	0.007	
nest phase	0.238	0.131	0.374	

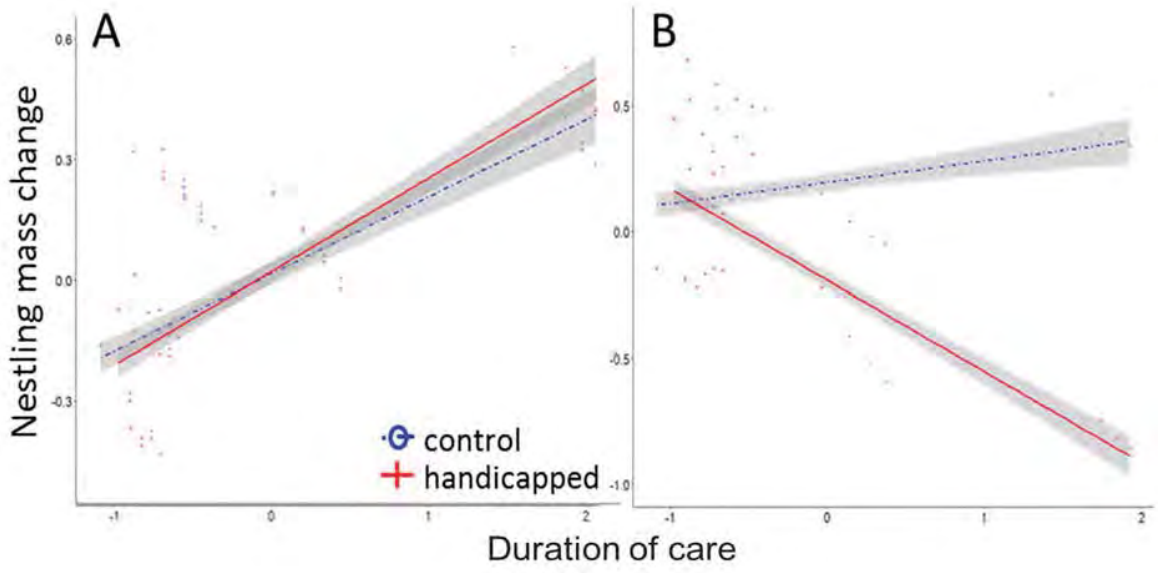

Figure 3. Standardized model-predicted changes in nestling mass varied according to duration of care: (A) The change in nestling mass did not differ between the handicapped and control groups in the pre-treatment phase (B) In the post-treatment phase, the mass of nestlings in the handicapped group decreased with an increasing duration of care, while the mass of nestlings in the control group increased with the duration of care. Shaded area represents 95% confidence interval.

Analyses of changes in nestling tarsus and wing growth (detailed in Tables S9-S12) indicated no treatment effects on either response variable. Both wing and tarsus growth changed over time, irrespective of treatment group, with nestlings having larger tarsus growth in the pre-treatment phase (estimate=0.59, 95%CI=0.26, 0.94, $p<0.001$), and larger wing growth during the post-treatment phase (estimate=-0.39, 95%CI=-0.78,-0.05, $p=0.042$). Tarsus growth also significantly decreased with an increasing duration of care (estimate=-0.58, 95%CI=-0.76,-0.43, $p=0.004$), independent of the treatment.

5.5 Discussion

Parental care is costly, and parents of iteroparous species are predicted to strive to minimize the costs that they incur in a current reproductive event to ensure future reproductive events (Williams 1966, Stearns 1992, Gross 2005). Our experiments demonstrate that, across 5 species, an increased cost of parental care generally results in a reduced visitation rate by the manipulated

parent, and that the additional costs are shared by its partner and their offspring. The strength of this effect was mediated by the duration of care that the offspring require; in large species with long care periods, the offspring were passed the largest share of the additional cost, while the partner increased their effort more in species with relatively short parental care periods. This result was evident in both changes to nest visitation rates of the parents and the body mass gain of the offspring.

Given the limited number of samples and species in this study, it faced several limitations. Responses may have varied according to factors we were unable to include due to a lack of statistical power and a lack of variation within the species included here. In particular, the scope of this study did not allow for examination of ecological factors; environmental unpredictability and a species' niche are likely to affect parental care decisions in ways that we were unable to test. For example, European bee-eaters are the only specialized aerial foragers among the species we tested, and consequently handicapped individuals may have accrued higher costs of foraging, particularly because gaps in flight feathers reduce flight maneuverability (Swaddle and Witter 1997). However, among the species included here, we only found differences in the compensatory behavior of partners rather than in the reduction of care by handicapped individuals. Thus, the effects of the handicapping treatment *per se* appeared to similarly influence the species included in this study. Moreover, it is possible that parents altered the quality or quantity of the food that they delivered to the nestlings, rather than the number of visits (Wright et al. 1998). Yet, changes in the condition of the nestlings matched the changes to total provisioning rates at the nest, indicating that costs were in fact accrued by nestlings with a handicapped parent. The findings of this study give novel empirical insight into the different strategies employed across species to deal with increased costs of parental care, but should be verified with larger-scale comparative studies. Such studies will be made possible with targeted experimental tests that manipulate parental care in a standardized way, so that comparable effect sizes are obtainable.

Little is known about the physiological effects of workload during parental care in free-living birds (Williams and Fowler 2015), but previous studies suggest that costs of parental care can be cumulative over a breeding cycle. Many bird species have been shown to rely (at least partially)

on nutrient reserves built-up prior to breeding and/or during incubation (Drent and Daan 1980, Martin 1987, Moreno 1989), in preparation for the costly provisioning stage of parenting. Thus, the workload during provisioning may be at or higher than the maximum sustainable workload (Weiner 1992, Low et al. 2012). If the maximum sustainable workload is exceeded over a long period, the risk of mortality is expected to increase (Drent and Daan 1980). Accordingly, parents are predicted to make decisions about parental care based on maintaining their physical condition above a threshold determined by the trade-off between offspring survival and their expected reproductive value at the end of breeding (Webb et al. 2002). Indeed, theory demonstrates that an increase in the daily energetic costs of care leads to a decrease in the duration of care in birds (Webb et al. 2002), and field data shows that species with long provisioning periods often have a greater loss of body mass than species with short durations of provisioning (Moreno 1989). Moreover, costs associated with extended parental care have been shown to have important carryover effects; for example, geese (*Branta bernicla*) with families in a given season are less likely to breed successfully in the following season (Inger et al. 2010). Taken together, these findings indicate that both the daily energy expenditure and the duration that expenditure must be sustained contribute to the overall costs of parental care.

Across all birds, large-bodied species with long care periods generally have low adult mortality (Speakman 2005, Valcu et al. 2014). However, in the set of species that we investigated, these traits were not highly correlated, thus we were able to tease apart where species lie on the spectrum of the trade-off between survival and reproduction. Here, the species with the largest opportunity for future reproduction differed from those with the longest burden of parental care. We expected that parents with a slow life history would be most sensitive to costs of reproduction (Williams 1966, Drent and Daan 1980, Linden and Møller 1989). However, only the duration of care but not life-history pace predicted the observed patterns in our study. The latter determined whether costs were passed to offspring while the former did not affect parental care decisions when faced with an increased cost of care. In accordance with our findings, a meta-analysis that looked explicitly at energy expenditure of handicapped birds found that a species' life history was

independent of whether individuals reduced investment into their own energy stores or their offspring's growth (Elliott et al. 2014).

Parents with low baseline costs of parental care probably have more leeway to increase their parental behavior without incurring deleterious consequences, and thus costs allocated to offspring can be minimized in these species. In contrast, parents with generally high costs of parental care are more likely to be at their maximum energetic capacity in a given reproductive event, and any increase in the costs associated with caring may have severe consequences in terms of future fitness and survival. Larger species do indeed expend more energy per day toward parental care than small species, however the ratio of energy expenditure to body mass tends to be smaller in large species (Masman et al. 1989). Thus, our results appear contrary to the prediction that large species expend the smallest share of their energy during parental care (Masman et al. 1989). However, this prediction is based on per-day calculations of energy expenditure relative to energy intake, and does not take into account the duration of care, which is generally longer for large species and thus may accrue higher reproductive costs over the whole breeding cycle.

Most studies of the costs of parental care focus on the trade-off between current and future reproduction or survival (intraindividual trade-offs, e.g., Owens and Bennett 1994, Webb et al. 2002, Alonso-Alvarez and Velando 2012, Santos and Nakagawa 2012), while relatively few studies have addressed the fitness consequences of parental decisions on current offspring (intergenerational trade-off, as discussed in Stearns 1989). Our results suggest that greater attention to intergenerational trade-offs is warranted, particularly in large species with long developmental (and thus parental care) periods. Moreover, our results indicate that, across species, parental care decisions may be weighed more against physiological workload constraints than against future prospects of reproduction, and support recent evidence that all bird species may devote comparable amounts of energy into survival, regardless of life history strategy (Santos and Nakagawa 2012, Elliot et al. 2013).

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5.6 Supplementary Material

Table S1. Correlation matrix, standardized principal components loadings, and communality (h2) of continuous species traits. Eigenvalues and cumulative variance explained by each component is given.

correlation matrix						loadings		h^2
	body mass	care time	family time	adult survival	reproductive allocation	PC1	PC2	
body mass	1	0.59	0.83	0.64	-0.28	**0.86**	0.47	0.97
care time	0.59	1	0.49	0.00	-0.16	**0.78**	-0.01	0.61
family time	0.83	0.49	1	0.24	0.10	**0.92**	0.03	0.84
adult survival	0.64	0.00	0.24	1	-0.51	0.20	**0.88**	0.81
reproductive allocation	-0.28	-0.16	0.10	-0.51	1	0.02	**-0.85**	0.73
eigenvalue						2.59	1.38	
cumulative variance explained (%)						0.45	0.79	

Table S2. Full mixed model results of effects on focal individual visitation rate.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.209	-0.320	0.672	0.263
duration of care	**0.796**	**0.242**	**1.204**	**0.022**
life history pace	**0.423**	**0.144**	**0.751**	**0.002**
brood size	0.257	-0.099	0.578	0.190
pre-treatment phase	-0.098	-0.476	0.230	0.588
treatment	**-0.465**	**-0.813**	**-0.104**	**0.006**
treatment x pre-treatment phase	0.386	-0.071	0.925	0.112
treatment x duration of care	-0.377	-0.765	-0.009	0.051
treatment x life history pace	0.255	-0.641	0.050	0.149
duration of care x pre-treatment phase	0.310	-0.141	0.709	0.173
life history pace x pre-treatment phase	0.027	-0.324	0.391	0.878
duration of care x pre-treatment phase x treatment	0.249	-0.277	0.788	0.345
life history pace x pre-treatment phase x treatment	0.124	-0.338	0.631	0.629
random effects				
species	0.186	<0.001	0.665	
nest	0.005	<0.001	0.029	

Table S3. Full mixed model results of effects on total visitation rate at the nest.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.215	-0.522	1.101	0.434
duration of care	0.704	-0.157	1.412	0.055
life history pace	**0.469**	**0.076**	**0.839**	**0.014**
brood size	-0.077	-0.334	0.165	0.537
pre-treatment phase	-0.106	-0.308	0.085	0.312
treatment	**-0.415**	**-0.712**	**-0.119**	**0.010**
treatment x pre-treatment phase	**0.303**	**0.013**	**0.595**	**0.047**
treatment x duration of care	-0.307	-0.607	0.012	0.069
treatment x life history pace	-0.184	-0.463	0.088	0.204
duration of care x pre-treatment phase	0.077	-0.128	0.296	0.490
life history pace x pre-treatment phase	-0.004	-0.204	0.163	0.929
duration of care x pre-treatment phase x treatment	**0.359**	**0.085**	**0.622**	**0.012**
life history pace x pre-treatment phase x treatment	0.138	-0.126	0.393	0.280
random effects				
species	0.701	<0.001	2.749	
nest	0.188	0.080	0.303	

Table S4. Mixed model results of effects on total visitation rates during pre-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.091	-0.705	1.002	0.767
duration of care	0.634	-0.208	1.484	0.108
life history pace	0.375	-0.095	0.845	0.084
brood size	-0.154	-0.457	0.107	0.271
treatment	-0.126	-0.403	0.160	0.363
treatment x duration of care	0.037	-0.237	0.300	0.782
random effects				
species	0.923	<0.001	3.488	

Table S5. Mixed model results of effects on total visitation rates during post-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.263	-0.668	1.230	0.394
duration of care	0.829	-0.082	1.597	0.065
life history pace	0.192	-0.393	0.656	0.414
brood size	-0.087	-0.435	0.251	0.675
treatment	**-0.455**	**-0.806**	**-0.122**	**0.008**
treatment x duration of care	**-0.348**	**-0.695**	**-0.025**	**0.040**
random effects				
species	0.741	<0.001	2.751	

Table S6. Full mixed model results of effects on nestling mass gain.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.140	-0.111	0.464	0.259
duration of care	0.054	-0.201	0.363	0.718
life history pace	0.275	-0.028	0.547	0.071
brood size	0.038	-0.165	0.242	0.706
pre-treatment phase	-0.168	-0.446	0.098	0.231
treatment	-0.296	-0.674	0.057	0.147
treatment x pre-treatment phase	0.300	-0.084	0.686	0.129
treatment x duration of care	-0.358	-0.687	0.063	0.074
treatment x life history pace	-0.079	-0.398	0.301	0.657
duration of care x pre-treatment phase	0.143	-0.140	0.403	0.333
life history pace x pre-treatment phase	-0.033	-0.275	0.258	0.837
duration of care x pre-treatment phase x treatment	**0.434**	**0.020**	**0.783**	**0.031**
life history pace x pre-treatment phase x treatment	0.060	-0.335	0.424	0.761
random effects				
species	0.006	<0.001	0.013	
nest	0.280	0.099	0.472	
nestling	0.002	<0.001	0.018	
nest-phase	0.249	0.128	0.379	

Table S7. Mixed model results of effects on nestling mass gain during pre-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.002	-0.263	0.282	0.984
duration of care	0.160	-0.113	0.411	0.222
life history pace	0.177	-0.019	0.388	0.084
brood size	-0.031	-0.251	0.186	0.786
treatment	-0.007	-0.321	0.341	0.974
treatment x duration of care	0.076	-0.234	0.418	0.637
random effects				
species	0.005	<0.001	0.008	
nest	0.392	0.229	0.600	

Table S8. Mixed model results of effects on nestling mass gain during post-treatment phase.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.254	-0.104	0.581	0.139
duration of care	0.102	-0.249	0.404	0.525
life history pace	**0.319**	**0.059**	**0.600**	**0.029**
brood size	0.138	-0.135	0.428	0.339
treatment	-0.391	-0.841	0.007	0.067
treatment x duration of care	**-0.421**	**-0.854**	**0.022**	**0.037**
random effects				
species	0.023	<0.001	0.058	
nest	0.724	0.482	1.026	

Table S9. Full mixed model results of effects on nestling tarsus growth.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	-0.253	-0.550	0.031	0.082
duration of care	**-0.540**	**-0.818**	**-0.258**	**0.006**
life history pace	-0.036	-0.306	0.236	0.820
brood size	0.055	-0.111	0.233	0.543
pre-treatment phase	**0.559**	**0.159**	**0.927**	**0.004**
treatment	0.125	-0.229	0.487	0.494
treatment x pre-treatment phase	-0.373	-0.897	0.162	0.153
treatment x duration of care	-0.044	-0.390	0.294	0.822
treatment x life history pace	0.051	-0.316	0.383	0.792
duration of care x pre-treatment phase	-0.214	-0.568	0.139	0.247
life history pace x pre-treatment phase	0.345	-0.007	0.679	0.057
duration of care x pre-treatment phase x treatment	0.339	-0.191	0.787	0.163
life history pace x pre-treatment phase x treatment	-0.250	-0.786	0.214	0.327
random effects				
species	0.024	<0.001	0.101	
nest	0.001	<0.001	0.007	
nestling	<0.001	<0.001	0.001	
nest-phase	0.529	0.393	0.687	

Table S10. Selected mixed model results of effects on nestling tarsus growth.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	-0.265	-0.536	0.045	0.055
duration of care	**-0.577**	**-0.758**	**-0.430**	**0.004**
life history pace	0.093	-0.099	0.276	0.288
brood size	0.056	-0.109	0.230	0.514
pre-treatment phase	**0.592**	**0.260**	**0.939**	**<0.001**
treatment	0.120	-0.201	0.464	0.490
treatment x pre-treatment phase	-0.368	-0.907	0.058	0.112
random effects				
species	0.024	<0.001	0.129	
nest	<0.001	<0.001	<0.001	
nestling	<0.001	<0.001	<0.001	
nest-phase	0.523	0.396	0.667	

Table S11. Full mixed model results of effects on nestling wing growth.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.250	-0.159	0.644	0.157
duration of care	0.085	-.257	0.405	0.604
life history pace	0.118	-0.171	0.407	0.431
brood size	-0.041	-0.221	0.225	0.641
pre-treatment phase	**-0.402**	**-0.766**	**-0.040**	**0.041**
treatment	-0.113	-0.469	0.239	0.560
treatment x pre-treatment phase	0.038	-0.512	0.534	0.871
treatment x duration of care	0.304	-0.061	0.662	0.110
treatment x life history pace	-0.023	-0.391	0.323	0.876
duration of care x pre-treatment phase	0.256	-0.123	0.592	0.176
life history pace x pre-treatment phase	0.014	-0.348	0.396	0.959
duration of care x pre-treatment phase x treatment	-0.155	-0.660	0.330	0.535
life history pace x pre-treatment phase x treatment	0.060	-0.438	0.537	0.820
random effects				
species	0.061	<0.001	0.253	
nest	0.005	<0.001	0.038	
nestling	0.001	<0.001	0.005	
nest-phase	0.573	0.408	0.731	

Table S12. Selected mixed model results of effects on nestling wing length.

		95% CI		
Effects	Estimate (β)	lower	upper	pMCMC
fixed effects				
intercept	0.290	-0.304	0.974	0.288
duration of care	0.073	-0.071	0.238	0.327
life history pace	0.110	-0.081	0.338	0.304
brood size	0.035	-0.246	0.282	0.774
pre-treatment phase	**-0.394**	**-0.779**	**-0.045**	**0.043**
treatment	-0.065	-0.401	0.289	0.706
treatment x pre-treatment phase	0.033	-0.480	0.580	0.910
random effects				
species	0.378	<0.001	1.22	
nest	0.003	<0.001	0.004	
nestling	0.001	<0.001	0.004	
nest-phase	0.565	0.405	0.712	

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Appendix

Reprint of relevant co-authored publication:

Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding

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Original Article

Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding

Szymon M. Drobniak, Gretchen Wagner, Emeline Mourocq, and Michael Griesser
Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, CH 8057 Zurich, Switzerland

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Cooperative breeding occurs in several major animal phyla, predominantly in arthropods and chordates. A number of comparative analyses have focused on understanding the evolution of cooperative breeding, yielding mixed, inconclusive, and often phyla-specific findings. We argue that much of this ambiguity results from an erroneous classification of social systems into noncooperatively and cooperatively breeding species. The shortcomings of this assumption are apparent among birds where noncooperative species constitute a heterogeneous group: some species are clearly non–family living, with offspring dispersing at or shortly after nutritional independency, whereas other species form persistent family groups through offspring delaying their dispersal substantially beyond independency. Here, we propose an objective, life history–based criterion classifying noncooperative bird species into non–family living and family living species. We demonstrate that by using the family time (the time offspring remain with its parent/s beyond independence) and body size–scaled reproductive investment, we are able to differentiate 2 groups with contrasting life histories. Our classification matches seasonal environmental variation experienced by different species: family living species postpone dispersal beyond the onset of less favorable autumn conditions. We discuss the consequences of this new social system classification for evolutionary and ecological research, potentially allowing solutions to some of the most intriguing riddles in the evolutionary history of birds—and cooperative behavior itself.

Key words: **comparative study, cooperation, dispersal, family breeding, life history, parental care, social system.**

INTRODUCTION

Understanding cooperation is fundamental to evolutionary biology, and this question was already seen by Darwin as a great challenge to his theory of natural selection (Darwin 1859). Hamilton's theory of kin selection (Hamilton 1964) resolved the apparent altruism of cooperation among related individuals and provided us with a framework to study the evolution of cooperation in kin groups and, particularly, its most interesting case—cooperative breeding. In many birds and mammals that breed cooperatively, young from previous broods remain with their parents beyond independence and help to raise younger siblings (Hatchwell 2009) although nonkin individuals can also engage in cooperative breeding (Riehl 2013).

Given the abundance of cooperative breeding in birds and mammals, and diversity of life histories and ecological covariates observed in both of these groups, they have served as model groups for studying the evolution of reproductive cooperation. In both groups, large-scale comparative analyses of cooperative breeding have been published recently, taking advantage of complete and accurate phylogenetic data available for birds and mammals (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2012; Feeney et al. 2013). In all of these studies, as well as preceding work (Arnold and Owens 1998; Cockburn 1998, 2003), social systems were described in a binary fashion: species were either classified as cooperative breeders, where individuals help raising offspring that are not their own, or as noncooperative, where only parents are involved in raising offspring. The presence of helpers is a straightforward criterion, easily observable in the field, and provides an unequivocal definition of cooperative breeding and could be further revised to account for kin-based and nonkin cooperation (Riehl 2013). However, this binary categorization fails to account for an important feature of animal social systems—namely the formation of kin groups in the absence of cooperative breeding.

Kin groups usually arise when offspring delay their dispersal beyond independency and remain with their parents and siblings for a given period of time (Russell 2000). In some cases, this period

Address correspondence to S.M. Drobniak. E-mail: szymonmarian.drobniak@uzh.ch.

(termed "family time" henceforth) is short, often short enough that such a strategy can be undistinguishable from dispersing right after reaching independence. However, in other cases, persistent family groups are formed, which usually is associated with various forms of nonreproductive kin cooperation (Dickinson and McGowan 2005; Griesser et al. 2006; Covas and Griesser 2007). A number of studies have pointed out that family living is an essential first step for the formation of cooperative breeding, as in almost all cooperatively breeding species offspring have first to delay dispersal and remain with their parents before they can become a helper at their parents' nest (Emlen 1994; Ekman et al. 2001, 2004). Thus, family living is likely to represent an intermediate strategy, fitting somewhere in the continuum of social systems between pair breeders and cooperative breeders. As such one might expect fundamental life-history differences between family living, non–family living, and cooperative breeding species and, consequently, merging non–family living and family living species might be partly responsible for equivocal and inconsistent results of comparative studies obtained so far (Covas and Griesser 2007; Griesser and Barnaby 2010). Yet, how should family living species be distinguished objectively from non–family living species?

Family time could provide a biological benchmark for this distinction. However, it would be too simplistic to classify as non–family living species only those where offspring disperse from parents, or parents abandon their offspring after reaching nutritional independence, as in many seabirds. Family times exhibit great variation and span from direct dispersal at independence to several years (Russell 2000). Species with short family time most likely are ecologically and evolutionarily more similar to species with zero family time. Thus, a threshold value of family time is needed in order to classify family living species. In such a way, a continuous measure directly describing the degree of parent–offspring association could be transformed into a categorical descriptor, supplementing the existing "cooperative breeding" category. The difficulty is finding an objective classification of this continuous quantity (i.e., family time) allowing to extract such threshold.

Here, we address the problem of defining family living by using a large data set of family time of nearly 750 bird species. We expect that evolution of delayed dispersal and family living would be associated with major changes in life-history traits, and thus, we predict that the footprint of these evolutionary processes should be visible in differences between family living and non–family living species. This evolutionary history would be reflected in a number of key eco-evolutionary traits associated with reproduction. Such traits could be used as benchmarks of life-history changes that arose due to breeding either in pairs or in larger family groups. However, such benchmark trait can only be used to measure differences between 2 groups. Locating the positions of the splitting point separating the groups requires a focal continuous variable that should be a straightforward extension of the desired nominal classification. An obvious choice in our case is the family time—as the trait directly measuring the degree of postindependence parent–offspring association. A more difficult task is finding a suitable benchmark variable, the values of which could guide us on the scale of focal variable.

To this end, we have used the body size–scaled initial reproductive investment (Sibly et al. 2012) as the benchmark variable of choice. We have used a simple numerical framework to define an objective threshold value of family time that best separates family and non–family living species. Breeding investment is closely related to individual fitness and integrates various ecological and physiological factors that together shape the life history of a species (Martin 1987; Martin et al. 2006; Sibly et al. 2012). It is regarded as an accurate proxy of species reproductive strategy, placing it on the important slow–fast life-history axis. Moreover, it is available for substantially more taxa than other life-history parameters and as such represents the most widespread fitness-related measure currently available. We not only demonstrate how family time can be tied up with reproductive investment to yield the desired classification of family/non–family living species but also discuss how our novel classification relates to the expected differences between non–family and family living species in terms of their life history and ecology.

MATERIALS AND METHODS

The key temporal variable used in our study was family time, defined as the period of time the offspring delayed dispersal and stayed with their parents after reaching nutritional independence. We used unpublished data from a review paper (Russell 2000) and the major handbooks of birds (Maclean and Robert 1985; Cramp et al. 1994; Poole 2005; Higgins et al. 2007; Del Hoyo et al. 2011) to collect data on the family time together with detailed information on the remaining temporal characteristics of bird breeding (incubation period, nestling time, time to independence after leaving nest). The data on the reproductive investment (annual sum of clutch sizes per breeding pair in each species scaled by the female body mass, see below) were retrieved from a recent publication (Sibly et al. 2012) while we also gathered additional values on reproductive investment from the literature (see above). In total, we had data on family time, reproductive investment, and egg mass for 712 species, covering all major clades defined by the low-level phylogenetic backbone derived by Hackett et al. (2008; see also Jetz et al. 2012 for more details). Deliberately we have removed cooperatively breeding species from all analyses—their status and classification do not require any additional clarification: a binary criterion exists (i.e., presence or absence of predominant reproductive cooperation) that unambiguously defines them as cooperating or otherwise.

We used a body weight–scaled key parameter of reproductive investment (productivity index; Sibly et al. 2012) calculated as:

$$\pi_m = \log\left(\frac{m_e n_e n_c}{m_f}\right),$$

where m_e is the egg mass, n_e the number of eggs per clutch, n_c the number of clutches per year, and m_f is the average female body weight. We adapted the productivity index proposed by Sibly et al. (2012) and used female body mass instead of male–female averaged mass, as the body weight of females—that is, the sex that physically produces the eggs—appears more appropriate as a reference for measuring reproductive investment. We repeatedly generated groups of family and non–family living species based on the family-time threshold varying between 2 and 150 days. Thus, we explicitly assumed that birds with family time < 2 days are classified as non–family living and species with family time > 150 days are classified as family living. We decided to stop at a family time of 150 days and classify all species with longer family times as family living for a number of reasons: 1) we do consider

species with family time >150 days as being certainly above the threshold and thus surely family living species and 2) beyond the 150 days threshold, the sample size in the 2 groups becomes very unbalanced as we successively classify more species as non–family living and less as family living (Supplementary Figure S1, for family time > 150 days, there are less than 25 species in family living group and more than 650 species in the non–family living group), which is likely to make the conclusion much less robust. For each of the 149 iterations, a mean productivity index (π_m) value was calculated for non–family and family living species. We then looked for the family-time threshold value that generates the maximum absolute difference in mean π_m between the 2 social systems.

To explore further how our categorization of social systems coincided with ecological conditions that might influence its evolution, we investigated the distribution of inferred social systems in relation to yearly seasonal changes and the mean growing season of the species distribution. The mean growing season describes overall plant vegetation timing in a given location (Michaletz et al. 2014) and strongly correlates with actual geographic location expressed as the absolute latitude of the centroid of species geographic distribution (Supplementary Figure S6). All models were analyzed using a generalized linear mixed model with a binomial distribution (a 2-state response variable: family living vs. non–family living; logit link function) in MCMCglmm (Hadfield 2010). The model included the phylogenetic effect to account for non-independence of species due to shared phylogenetic history. All runs were performed with 1 000 000 iterations, 250 000 burn-in period, and samples taken from the posterior distribution of estimated fixed and random effect parameters every 1000 iterations (resulting in effective sample size of approx. 1000). Phylogenetic signal was calculated as the intraclass correlation coefficient at the level of the phylogenetic random effect according to Hadfield (2014).

In order to ensure that the results are valid and do not result from statistical artifacts, we have performed a number of validations based on simulation and bootstrapping. The details on each of the validation methods can be found in the Supplementary Materials and methods.

It is difficult to construct analytically sampling error measures for the estimated parameter. First, randomizing/resampling the data tends to generate functional relationships of several kinds between the difference in π_m and family-time threshold (depending on the iteration we were able to fit, e.g., logistic, polynomial, exponential to the resulting pattern). Thus, automatically extracting the threshold value—which could be used to construct approximate sampling distribution—is difficult. To provide a surrogate of sampling distribution, we have used the following strategy: 1) we generated 1000 subsets of data by bootstrapping (resampling with replacement) rows of original data set; 2) for each subset performed threshold search; 3) fitted a segmented piecewise regression to the resulting pattern (package segmented; Muggeo 2003) to extract the breaking point of the pattern, indicating the maximum observed value (most patterns either plateau or reach maximum at this value; in both cases, the breaking point accurately identifies the threshold—in case of the original pattern—Figure 1—this breaking point is equivalent to edge of the plateau, i.e., family time = 50 days); 4) constructed a sampling distribution of 1000 estimated breaking points, which will necessarily be centered around the original estimated threshold.

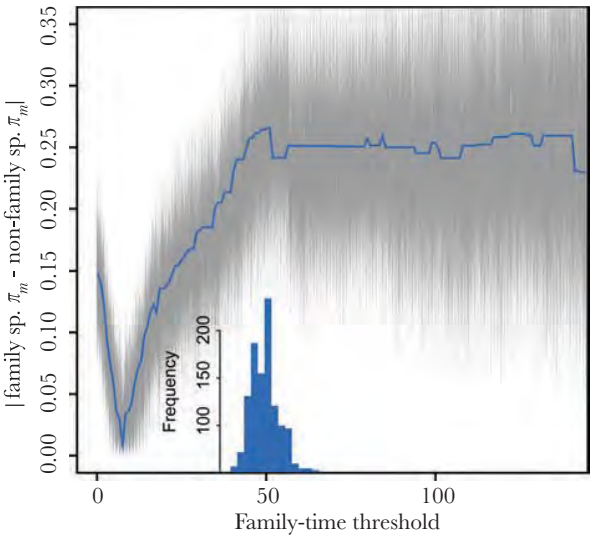

Figure 1
Difference in annual mass–scaled productivity index (π_m) between family living and non–family living species in relation to the family-time threshold used to differentiate the 2 groups. Blue line represents original pattern, and gray lines depict patterns obtained for bootstrapping samples drawn from the data. The approximate sampling distribution of the threshold value of family time is shown as a histogram on the horizontal axis.

RESULTS

The shifting-threshold approach indicated a maximal difference in initial breeding investment between resulting non–family and family living species for a cutoff value of 50 days (Figure 1). Using this 50-day threshold resulted in 529 species classified as non–family living and 104 species being classified as family living. The remaining 79 species are cooperative breeders and were not included in our analyses as the definition of cooperative breeding is unambiguous. Bootstrapping of family-time values reveals noise around the original pattern, mostly generated by resampling random species from a continuum of family times—vast majority of samples, however, successfully replicate the 50-day threshold (see histogram, Figure 1).

Four different validation methods all supported the 50 days threshold (see Supplementary Materials and methods). In particular, phylogenetically corrected values recapitulated the pattern observed in raw means (Supplementary Figure S1). Randomized samples (see Supplementary Materials and methods: validation 2 and 3) did not exhibit the pattern observed in the original data (Supplementary Figures S2 and S3). Moreover, the pattern also was confirmed when equal sizes of social system groups were used by resampling them for each threshold value with replacement (see Supplementary Materials and methods: validation 4 and Supplementary Figure S5). It is important to note that the choice of the start of the plateau in Figure 1 is only one possibility. One might argue that instead of using the first observed plateau observation, it might be more suitable to shift the threshold further along the plateau toward greater values of family time or place it at some other unambiguous points along the estimated line (e.g., the inflection point located between 10 and 50 days of family time, equivalent to roughly a half of maximum observed difference between family and non–family breeding species). However, any other placement of the threshold would result in a less parsimonious conclusion (putting the threshold further on the plateau would result in

including as non–family breeding individuals those that do not contribute to predicted differences in reproductive allocation and at the same time have abnormally long family times) or in classification that is not stable in terms of life-history parameters (putting the cutoff at the inflection point would yield where differences between the 2 resulting groups would be very sensitive to even small changes of the chosen classification threshold).

Independently of family-time considerations, an interesting effect concerning total breeding period became apparent in our data. Combined data on incubation and nestling time with the time to independence and family time indicated that in most non–family living species, offspring dispersed the latest 150 days after the onset of breeding (Figure 2). In contrast, in the majority of family living species, dispersal of offspring occurred later than 150 days after the onset of breeding (Figure 2). In non–family living species, offspring dispersal occurred later than 150 days in only 14 cases and the majority of those species have the centroid of their geographical distribution in low latitude regions (Figure 3). Similarly, the majority of family living species where offspring disperse before 150 days from the start of breeding (n = 24 species) occurred mostly in temperate regions or resided in both temperate and tropical climate (Figure 3). This was further confirmed by an interaction between total breeding period (total time from egg laying to offspring dispersal) and the mean growing season of the species distribution in a mixed model looking at the probability of observing a particular breeding system (Supplementary Table S1). The interaction indicates that the probability of being a family living species increases with total time spent with parents (sum of all predispersal periods) in regions of long mean growing season (i.e., low latitudes) but decreases with increasing total time spent with parents in regions where the mean growing season is shorter (i.e., latitude increases) (Supplementary Table S1). The generalized mixed model confirmed that the social system (family living vs. nonfamily breeding) is highly phylogenetically structured

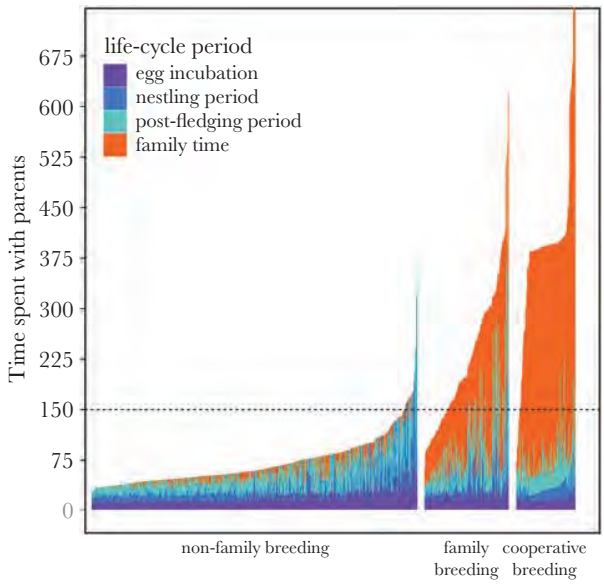

Figure 2
The distribution of total times that offspring spend with their parents, subdivided into respective periods of the lifecycle and in relation to 3 categories of social breeding defined using our approach. The 150-day limit is indicated with a dashed line (see Discussion for more details).

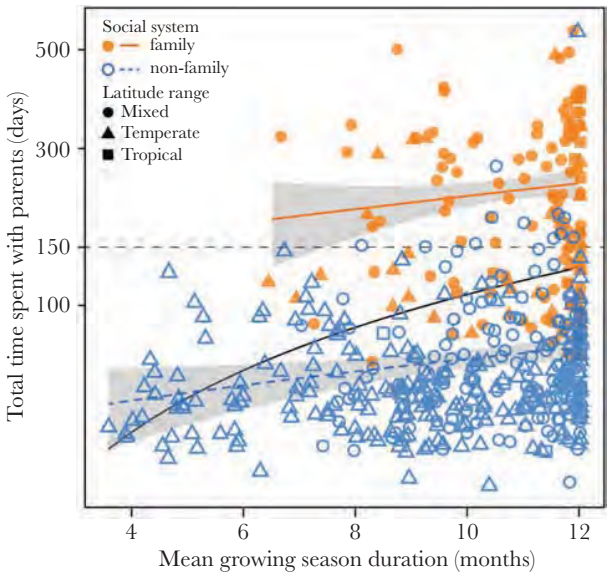

Figure 3
Association between the total time offspring spent with their parents (from onset of incubation to dispersal, in days), the mean growin season of species distribution, and the range of latitudes occupied by each species. The line lacking confidence band depicts overall relationship in all species, the two lines with confidence bands show relationships in the 2 social breeding systems. The 150 day cutoff (see text) is indicated with a dashed horizontal line.

(phylogenetic heritability and its 95% highest posterior density interval—on the link function scale: 0.67 (0.54; 0.87); on the scale of data: 0.94 (0.87; 1.06)).

The estimated threshold that we use to categorize social systems in birds coincides with a natural hiatus in the distribution of family times (Figure 4). Excluding family times equal to zero, the distribution is bimodal with a ridge around the value of 50 days (Figure 4). Interestingly, when including zero family times, the distribution is trimodal as most species tend to disperse directly after achieving independence. This first gap separates species having zero and nonzero family time and thus, for reasons explained in the Introduction and the Materials and Methods, cannot be used as a suitable threshold to define families.

DISCUSSION

Our results confirm that social breeding systems are more heterogeneous than previously appreciated (but see Russell 2000). Using birds as a model system and a central life-history trait, the annual reproductive investment, we demonstrate that noncooperatively breeding species are heterogeneous in terms of the postindependence offspring dispersal and can be further divided into 2 distinct categories. One of the most easily observable features of social breeding—namely, the formation of persistent groups composed of kin individuals delaying their dispersal—occurs also in species lacking any traces of reproductive cooperation. However, contrary to reproductive cooperation, classifying family living species is more ambiguous as it cannot be assessed based on a bicategorical descriptive behavior. The fact that offspring in some species remain some time beyond independency with their parents may just reflect variation in dispersal timing as found in many species, or behavioral inertia in moving from one phase of

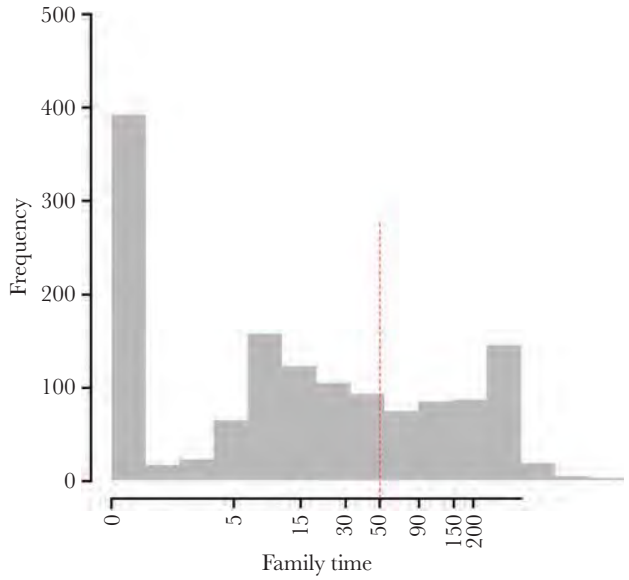

Figure 4
Distribution of family times in 1103 bird species. Dashed line indicates the 50-day family-time threshold that was chosen to separate family living and non–family living species.

life cycle to the other, particularly if short delays in dispersal are costly to neither parents nor offspring. Our approach provides an objective way of finding the critical family-time value that results in the biggest difference between the 2 social systems. Moreover, the result coincides with naturally observed discontinuity in the distribution of family times in our larger set (i.e., including species for which we did not have the productivity index and that could not be included in the main analysis). Although similar considerations relating delayed dispersal and breeding ecology have been made in evolutionary biology (e.g., Russell et al. 2004), our approach is unique in providing an actual definition that is based on measurable properties of bird reproductive biology. Importantly, our analyses have proved to be robust to all statistical artifacts that might generate similar results—all validation procedures confirmed the presence of the observed pattern and supported its uniqueness (in both randomization analyses that break association between productivity and family time, the pattern disappeared).

Annual productivity (π_m) is a central and fundamental life-history variable (Sibly et al. 2012), reflecting adaptations of bird life histories to varying ecological conditions (Lack 1968; Griebeler et al. 2010; Sibly et al. 2012). Thus, it is also affecting the link between social systems and reproductive strategies (Emlen 1994; Arnold and Owens 1998; Cockburn 1998; Covas and Griesser 2007). Splitting non–family living and family living species according to a threshold value of family time equal to 50 days maximizes the difference in annual investment observed in these 2 groups. On average, non–family living species have a higher annual productivity compared with family living ones, confirming studies indicating that delayed dispersal is more frequent in species with low adult mortalities and low reproductive output (Arnold and Owens 1998; Ekman et al. 2001; Russell et al. 2004). The difference is substantial—non–family living species produce on average 1.5 times more eggs per year per unit of body mass than family living taxa. It is possible that the strategy of forming family groups buffers out costs of rearing offspring and results in being able to maintain similar overall success with a lower annual productivity. Alternatively, delayed dispersal, while being beneficial to the offspring, may be costly for parents—forcing them to decrease their reproductive output considerably and favoring offspring quality over quantity. Although our study does not point to one particular alternative, we hope it will stimulate further research toward understanding costs and benefits of family living.

Why is the 50-day threshold a biologically meaningful cut-off to define family living? In nontropical climatic zones, the period of year comprising the most favorable conditions for breeding spans over approx. 150 days (rounded to full months; mean 155.72 ± 10.49 days [www.weatherbase.com, accessed 5 December 2014]; favorable conditions defined as months with average temperature greater or equal to 11 °C, the temperature associated with an average large-scale vegetation onset in temperate locations and the start of the optimal photosynthetic activity; Morison and Morecroft 2006) and starts roughly in April/May in the northern hemisphere (respectively in September/October in the southern hemisphere), concluding with a decrease in food abundance and an onset of less favorable conditions in September in the northern hemisphere (respectively March in the southern hemisphere) (Morison and Morecroft 2006). For most non–family living species, the total breeding period is shorter than 150 days (Figure 2) and hence does not progress beyond this boundary of worsening conditions. The total breeding period of most family living birds, however, exceeds 150 days (Figures 2 and 3). The outcome of our analysis reveals an ecological footprint of the evolution of family living with respect to seasonally occurring unfavorable conditions (Russell 2000). Delaying dispersal beyond autumn may only be possible in species where offspring can benefit from prolonged association with their parents, increasing their survival (Ekman et al. 2001; Covas and Griesser 2007). Our approach indicates that these benefits may outweigh costs of family living only if it is associated with long-enough association of individuals forming a family group.

Relating family and non–family living to the assumed 150 days period of unfavorable conditions (Figure 3) reveals yet another interesting biogeographical pattern: all pair-breeding species that live in high latitudes lie below this line, whereas all the remaining (pair and family breeding) species laying above this line live exclusively in mid- and low latitudes. Thus, prolonged parental care and delaying dispersal seem to be ecologically constrained in high latitudes but provide clear advantage in lower latitudes, shifting the distribution of kin-group forming species toward lower latitudes (Russell 2000). The nature of this constraint requires further research: it is possible that solely climatic constraints prevent birds from delaying dispersal into harsher and less viable conditions; however, other factors contributing to delayed dispersal (e.g., access to high-quality territories inherited from parents) also may be latitude constrained.

Interestingly, in both groups, there are species that do not match this 150-day criterion. Apart from random noise in the data (i.e., inaccurate data on family time—or timing of any other part of the reproductive cycle), such cases may be explained by accounting for geographical distribution of such species. Most non–family living species crossing the 150 days' timeline come from low absolute latitude regions (i.e., tropical/subtropical) or are widespread species with mixed climatic preferences. Similarly, family living species with total breeding period below 150 days tend to be temperate

climate ones. Thus, mismatches occur mostly in cases where the 150-day threshold may not be accurate and limiting, supporting our result.

The consequences of this new classification for our understanding of the evolution of social behavior in birds still remain to be explored. Our preliminary results not presented here indicate that discrepancies between the traditional and new classification of social breeding systems are substantial. For example, our classification significantly alters observed associations between social system and environmental unpredictability in terms of environmental dependency of cooperative breeding, extending and greatly clarifying earlier analyses (e.g., Jetz and Rubenstein 2011). Our analyses indicate that merging together nonfamily and family breeders erroneously associates 2 very different strategies, and in terms of environmental sensitivity, family breeders are more similar to cooperative breeders (Griesser et al. 2014). Moreover, family living taxa exhibit markedly higher levels of sexual body size dimorphism compared with non–family living and cooperatively breeding species, which emphasizes the great evolutionary uniqueness of family breeding in terms of sexual selection pressure and how it is related to overall life-history patterns in birds (Drobniak et al. 2014).

To conclude, our life-history-based approach shows that cooperative breeding and non–family living are not the only alternatives on the scale of social modes in birds. Family living in the absence of cooperative breeding represents an intermediate state, which hitherto has not received sufficient attention. More importantly, family living may represent a transition stage in the evolution of cooperative breeding as almost all cooperative breeding birds live in family groups (Riehl 2013). Using family living as an intermediate social system, one can provide a more parsimonious, multistage description of how cooperative breeding might have evolved in birds (Emlen 1994; Ekman et al. 2004; Covas and Griesser 2007). Appreciating this social system will open new research perspectives and solve existing inconsistencies in our understanding of the evolution of cooperation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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